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SPECIAL SECTION: BACK TO THE FUTURE OF RESERVOIR FISHERIES MANAGEMENT—WHAT HAVE WE LEARNED IN 50 YEARS?

Alabama Bass Alter Reservoir Black Bass Species Assemblages When Introduced Outside Their Native Range

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Abstract

Black bass *Micropterus* spp. stocked outside of their native range have often been implicated in declines of native fishes, but impacts of these stockings on native congeners have been examined less commonly and almost never in reservoirs. Relative abundance and creel data were obtained from seven reservoirs (632–13,156 ha) in four southeastern states where Alabama Bass *M. henshalli* had been illegally stocked. Genetics data for black bass were collected in nine more reservoirs in five southeastern states where similar introductions occurred. In each case, Alabama Bass introduction was swiftly followed by sweeping changes in the black bass composition. Largemouth Bass *M. salmoides* relative abundance declined by 42–77% after Alabama Bass introduction in four of five reservoirs, but total black bass relative abundance was unchanged in three of them, indicating that Alabama Bass essentially replaced Largemouth Bass. Alabama Bass or their hybrids dominated the black bass genetic sample in five of nine reservoirs, and pure specimens of non-Alabama Bass species composed <50% of the sample in six of nine reservoirs. Smallmouth Bass *M. dolomieu* were virtually extirpated via hybridization with Alabama Bass in two of the study reservoirs, and genetically pure fish were rare in several others. These changes occurred over relatively short time intervals, often within 10 years after detection of Alabama Bass, stressing the need for continual vigilance via routine monitoring and a proactive public relations campaign to discourage and limit new introductions. The leading edge of the Alabama Bass invasion now encompasses several notable Smallmouth Bass fisheries in North Carolina and is on the border of numerous others in Tennessee, Virginia, and beyond. The spread of nonnative black bass, such as the Alabama Bass highlighted in this article, constitutes one of the greatest threats to conserving native black bass fisheries.

Introduction of nonnative fishes is a leading cause of native fish imperilment worldwide (Gido and Brown 1999; Cambray 2003; Hulme 2006). The rate of species introductions has increased through time; in North America, hundreds of exotic plants and animals became established in aquatic communities during the 20th century (Ricciardi and Rasmussen 1998). Invasion rates have increased over the first two decades of the 21st century, as global trade has expanded and provided more opportunities for intercontinental movement of nonnative species (Cambray 2003; Hulme 2006; Russell and Blackburn 2016; Davis and Darling 2017). Once established, nonnative species can drastically impact freshwater ecosystems, replacing or reducing native species, altering food webs, and destroying habitat (Gido and Brown 1999; Hulme 2006; Cucherousset and Olden 2011; Trumpickas et al. 2011). Established populations of nonnative fishes also provide a source or opportunity for further expansion to new areas, either via connected waterways or through anthropogenic assistance (Cambray 2003; Rahel 2005; Davis and Darling 2017; Peoples and Midway 2018).

Nonnative species are often introduced for a specific purpose, such as to create new angling opportunities or to provide a nearby source of familiar food fish (Gido and Brown 1999; Cambray 2003; Ellender et al. 2014; Davis and Darling 2017; Peoples and Midway 2018). Historically, many of these introductions were conducted by governmental agencies (Fajen 1976; Keith 1986; Townsend 1996; Cambray 2003; Ellender et al. 2014; Long et al. 2015). As biologists began quantifying biodiversity loss due to nonnative introductions, the stocking of new species by agencies as a form of fisheries enhancement became less common and mostly ceased by the 21st century (Hulme 2006; Slaughter 2015). However, as agencies reduced or eliminated these programs, the general public stepped in to fill the void (Koppelman 2015; Dorsey and Abney 2016; Davis and Darling 2017; Peoples and Midway 2018). Although many countries have enacted legislation against this practice, the strength of these laws varies widely worldwide and even within countries (Britton et al. 2011; Ellender et al. 2014). Regardless, enforcement of existing laws is notoriously difficult, as introductions can be easily accomplished at public access points quickly and unobtrusively (Rahel 2005; Koppelman 2015).

Most introductions of nonnative fishes fail, either due to a lack of adequate habitat, thermal tolerance exceedance, an insufficient number of fish introduced, or competition with existing species (Ricciardi and Rasmussen 1998; Britton et al. 2011). Likewise, only a small percentage of successful introductions results in significant impacts to native species or ecosystems (Gido and Brown 1999; Hulme 2006; Britton et al. 2011). However, some introductions have resulted in enormous ecological and economic consequences, including introductions of Common Carp *Cyprinus carpio*, catfishes (Ictaluridae), and Rainbow Trout *Oncorhynchus mykiss* (Ricciardi and Rasmussen 1998; Perry et al. 2002; Miller and Crowl 2006; Britton et al. 2011). Most research on invasive aquatic species (IAS) has been focused on quantifying the extent of conflicts with native species in lieu of delivering robust solutions and rarely addresses all stages of the invasion process (Hulme 2006). The consensus of numerous synthesis studies on IAS has been that the most successful invaders are species with large body sizes, young age at maturity, high fecundity, and shorter maximum life spans (Ricciardi and Rasmussen 1998; Liu et al. 2017; Peoples and Midway 2018). Additionally, certain habitats are more vulnerable to invasion, particularly habitats characterized by high environmental variability or those suffering from significant abiotic disturbances (Gido and Brown 1999; Whittier and Kincaid 1999; Hulme 2006). However, primary drivers of introduction success tend to be more about the pathway to the introduction rather than specific species traits or characteristics of the receiving waters (Hulme 2006). Broadly termed "propagule pressure," the basic premise is that the more frequently or easily a species is introduced into new water bodies, the higher the likelihood of successful establishment (Cambray 2003; Hulme 2006; Davis and Darling 2017; Peoples and Midway 2018). Overall, our ability to accurately diagnose or predict the introduction success of a given species or the potential for a species to become invasive lags far behind the rate of new introductions (Cambray 2003; Hulme 2006; Britton et al. 2011).

Black bass *Micropterus* spp. are the most popular sport fish in the United States and have been widely introduced outside of their native range in North America and across the world (Jackson 2002; Shaw 2015; Slaughter 2015). Like most centrarchids, many members of this genus are highly adaptable to a wide range of aquatic systems and are tolerant of degraded habitat conditions (Shaw 2015); however, a few species are more specialized, are endemic to lotic systems in specific river basins, and do not withstand impoundment conditions (Curtis et al. 2015; Leitner and Earley 2015; Nagid et al. 2015; Sammons et al. 2015). More widespread black bass species often thrive in reservoirs, where they provide robust and economically important fisheries (Driscoll and Myers 2014; Rider and Maceina 2015; Shaw 2015). However, when stocked outside of their native range, black bass have been implicated in the loss or decline of many small-bodied native species (Whittier and Kincaid 1999; Moyle et al. 2003; Trumpickas et al. 2011; Ellender et al. 2014).

Native ranges of black bass often overlap, and commonly, multiple species share water bodies with little to no obvious negative interactions (Buynak et al. 1989; Scott and Angermeier 1998; Sammons and Bettoli 1999; Johnson et al. 2009; Goclowski et al. 2013). However, problems typically arise when a species is moved outside of its native range and into the range of another black bass. In those cases, biologists have observed high rates of introgression and sometimes complete exclusion of one or more species (Avise et al. 1997; Barwick et al. 2006; Littrell et al. 2007; Koppelman 2015; Dorsey and Abney 2016). Most of these issues have been documented in lotic systems; few similar impacts have been observed in reservoirs or other lentic systems. However, introduction of nonnative Alabama Bass *M. henshalli* into several reservoirs of the Savannah River basin in South Carolina and Georgia resulted in almost complete loss of "Bartram's Bass" *M.* sp. cf. *coosae* (Barwick et al. 2006; Leitner et al. 2015; Bangs et al. 2018). Likewise, illegal introduction of Alabama Bass into several Georgia reservoirs resulted in the almost complete loss of native Smallmouth Bass *M. dolomieu* fisheries through introgressive hybridization (Avise et al. 1997; Pierce and Van Den Avyle 1997). These events have been rare and confined mostly to watersheds adjacent to the Mobile River basin, the native range of Alabama Bass (Rider and Maceina 2015). However, introductions often are not detected until long after they occur due to their clandestine nature and the difficulty of identifying black bass hybrids in the field (Lewis et al. 2021). Until recently, genetic sampling of black bass was rare except for specific reasons, such as broodstock collection (Slaughter 2015), further allowing the spread of nonnative fish to occur without being noticed by fisheries management agencies.

Introduction of nonnative Alabama Bass into Lake Norman, North Carolina, in 2001 resulted in a rapid decline of native Largemouth Bass *M. salmoides* and a concomitant increase in Alabama Bass over a 10-year period (Dorsey and Abney 2016). Reports of new introductions of Alabama Bass in North Carolina prompted biologists to examine other water bodies to assess the effects of this species on reservoir black bass fisheries. Similar reports prompted agency biologists in adjacent states to assess the situation in their waters. Currently, Alabama Bass are not on most IAS lists at the state or federal level, but if a recurring pattern of displacement or replacement of native or other desirable black bass fisheries by this species can be established, then a more proactive approach might be taken. Therefore, the objectives of this study were to (1) examine changes in relative abundance of Largemouth Bass in relation to Alabama Bass introduction in five reservoirs of the southeastern USA, (2) examine changes in angler harvest of Largemouth Bass in two more southeastern U.S. reservoirs relative to the introduction of Alabama Bass, and (3) assess the genetics of black bass populations in nine other reservoirs as related to Alabama Bass introductions.

METHODS

Study species.— Formerly considered a subspecies of Spotted Bass *M. punctulatus*, the Alabama Bass was elevated to the species level by Baker et al. (2008). The species is native to the Mobile River basin in Alabama, Georgia, Mississippi, and Tennessee and has been introduced into waters of central and southern California and Texas by state agencies (Rider and Maceina 2015). Further, in the 1980s, Alabama Bass were illegally introduced into reservoirs in northern Georgia and South Carolina (Pierce and Van Den Avyle 1997; Barwick et al. 2006), where they subsequently migrated throughout most of those basins and threaten native black bass in those habitats (Sammons et al. 2015; Bangs et al. 2018;

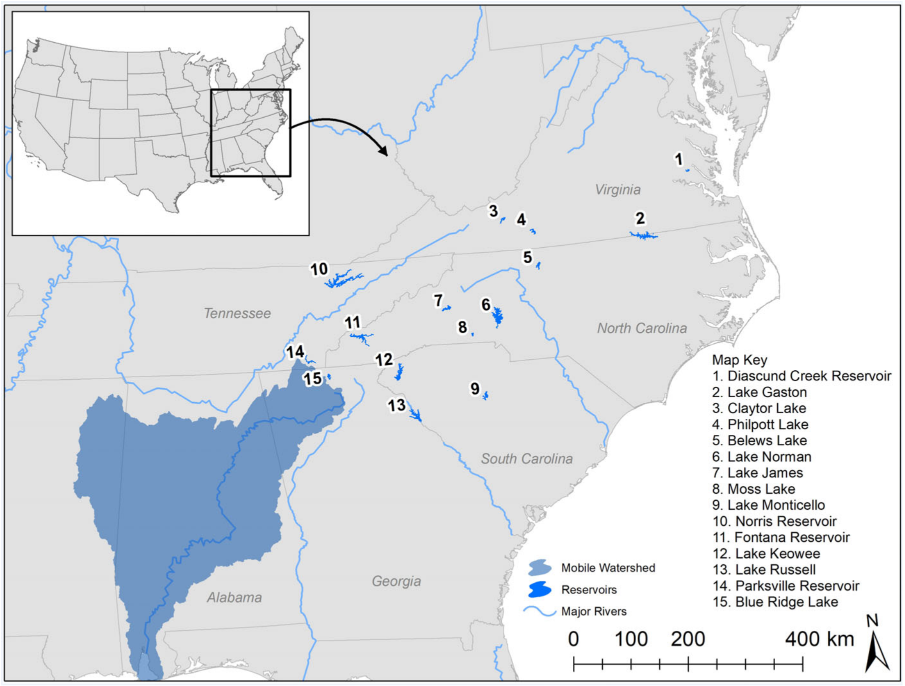

FIGURE 1. Map of the southeastern United States, showing all study sites where black bass relative abundance or genetics data were collected for this study. The shaded area represents the native range of Alabama Bass (i.e., the Mobile River basin).

Peoples et al. 2021). Alabama Bass are highly adaptable to a wide range of habitat conditions, being found in streams, rivers, and reservoirs (Rider and Maceina 2015). In reservoirs, Alabama Bass appear to be more abundant than sympatric Largemouth Bass in deeper reservoirs with abundant rock substrate and clear water (Greene and Maceina 2000; Rider and Maceina 2015). The species grows quickly, usually at rates similar to those of Largemouth Bass, and likely matures at similar ages as well (Rider and Maceina 2015). Alabama Bass support popular and economically important fisheries throughout much of their native range, and they often comprise most of the black bass caught by recreational anglers in these systems (Rider and Maceina 2015).

Data sources.— Black bass catch-per-effort (CPE) data were obtained from five reservoirs in three states to examine trends in catch before and during Alabama Bass introduction and subsequent expansion (Figure 1). Relative abundance (as CPE) sampling was conducted over a 31-year period from 1991 to 2021, but because not every reservoir was sampled in each year, the number of reservoir-years of data varied from 7 to 31 across systems (Table 1). Blue Ridge Lake and Lake Norman had the largest data sets (31 and 26 reservoir-years, respectively), whereas the other three had only 7–10 reservoir-years of data (Table 1). The earliest documentation of Alabama Bass collected in samples was in 1999 for Blue Ridge Lake, followed by Lake Norman and Parksville Reservoir in 2001. The most recent Alabama Bass introduction documented in these study reservoirs was in 2011 for Belews Lake, North Carolina (Table 1).

Long-term data sets existed for black bass relative abundance in Blue Ridge Lake, Lake Norman, and Belews Lake, whereas in Parksville Reservoir and Moss Lake, black bass CPE data were collected to examine trends in black bass catch once Alabama Bass introduction was detected and during subsequent expansion (Table 1). Lake Norman was the subject of a previous study by Dorsey and Abney (2016); the present study uses their original data set (1993–2013) and expands upon it with more recently collected data to follow black bass CPE trends up to 2019. In all reservoirs, black bass were sampled using spring electrofishing along shorelines via multiple transects that were either delineated by time or shoreline length and were fixed or haphazardly chosen each year, depending on the managing agency's standard protocols (Table 1). The number of sites, number of dip-netters, box settings, and sample site lengths all varied among agencies and even among reservoirs within states but were consistent within each reservoir across the time frame of this study. Although no attempt was made to conform sampling protocols to the "North American Standard" proposed by Bonar et al. (2009), by happenstance most protocols fell in line with those recommendations. However, given that CPE was only compared across years within reservoirs and not across reservoirs,

TABLE 1. Basic characteristics and sampling schemes used to collect black bass via spring electrofishing from five reservoirs in the southeastern United States. The state where each reservoir is located is indicated in parentheses. Range of years in which each reservoir was sampled (with the number of years sampled shown in parentheses), number of sample sites, whether sites were fixed or chosen haphazardly, and sample effort are also provided. Year of first documentation of Alabama Bass (year of first ALB) in each reservoir represents the year during which the species was first collected in samples; years in parentheses denote earlier reports of the species from other sources.

Reservoir	Area (ha)	Mean depth (m)	Years sampled	Sample sites	Sample effort (transect length or time)	Year of first ALB
Belews Lake (NC)	1,654	14.6	2007–2021 (6)	11–21 fixed/haphazard	300 m	2014 (2011)
Blue Ridge Lake (GA)	1,331	18.0	1991–2021 (31)	10 fixed	30 min	1999 (1993)
Moss Lake (NC)	672	15.2	2008–2021 (10)	5 fixed	300 m	2008 (2006)
Lake Norman (NC)	13,156	10.2	1993–2019 (26)	30–64 fixed/haphazard	300 m	2001
Parksville Reservoir (TN)	781	13.7	2001–2022 (11)	10–12 haphazard	15 min	2001

differences in sampling protocols among reservoirs were not expected to affect the results of this study. Sampling stations were generally chosen to provide the greatest range of spatial coverage and to sample all representative habitats for black bass. Black bass CPE was expressed in fish per hour for all reservoirs where sampling was conducted using timed transects. In Moss and Belews lakes, fish were sampled along 300-m transects, but biologists also recorded effort in seconds, allowing CPE to be expressed as fish per hour. In Lake Norman, time was not recorded; thus, CPE was expressed as fish per 300 m.

Alabama Bass were introduced into Lake Keowee and Richard B. Russell Lake (hereafter, “Lake Russell”), two reservoirs within the Savannah River basin in South Carolina and Georgia (Figure 1), during the mid to late 1980s (Leitner et al. 2015). Standardized electrofishing data were unavailable for either reservoir, but angler harvest of black bass in both was estimated by South Carolina Department of Natural Resources (SCDNR) personnel using a roving creel survey from 1980 to 2020. These data were used as a surrogate to track population trends of black bass, as catch and harvest data obtained via creel surveys are usually considered to be related to population trends (Jones and Pollock 2012). Surveys were designed with nonuniform probabilities and a stratified random sampling design as described by Malvestuto et al. (1978). The calendar year sample period was divided into four seasonal time blocks of 3 months each. Spring and summer time blocks were sampled more frequently based on seasonal fishing effort from previous creel surveys. Dates and times were randomly selected for each sample period and were stratified by day type (weekday or weekend day/holiday); times were stratified by season. Approximately 40% of all creel samples were conducted during the weekend/holiday time block. In Lake Keowee, all seasonal blocks had AM and PM time periods that were assigned probabilities of 0.40 and 0.60, respectively. In Lake Russell, fall (October–December) and winter (January–March) seasonal blocks had two time periods with the same probabilities used for Lake Keowee, but the spring and summer seasonal blocks had three time periods: AM, noon, and PM, with sample probabilities of 0.40, 0.10, and 0.50, respectively.

Creel surveys were also geographically stratified to detect spatial differences in angler catch and harvest and to allow reservoir-wide data expansion. Each zone was assigned an equal probability of being sampled in the random selection process. Surveys were conducted within a section by making either a right or left complete circuit of the stratum, with the direction determined by coin toss. The creel clerk conducted an instantaneous count of actively fishing anglers and conducted as many interviews as possible during the time block. Another coin toss determined whether the creel clerk conducted the instantaneous count circuit or the interview circuit first. Fish in angler creels were identified to species and counted. Because Largemouth Bass and Alabama Bass are easily distinguished by the presence of a tooth patch (Baker et al. 2008) and given that hybrids between these species are rare (Bangs et al. 2018), trained creel clerks were expected to be able to easily identify the species in the angler creels.

Another nine reservoirs in Tennessee, South Carolina, North Carolina, and Virginia were sampled to determine black bass genetics from 2017 to 2021 (Figure 1). The objective of each survey differed among reservoirs at the biologists' discretion. Some reservoirs were sampled to assess the genetic integrity of specific black bass species, whereas others were sampled to assess the current level of hybridization within black bass species other than Largemouth Bass; in Lake Monticello, South Carolina, genetics were assessed during broodstock collection for Smallmouth Bass. In each case, biologists collected samples from all fish that were field-identified as the target group up to a specified maximum sample size or effort. Most reservoirs were only sampled once over this period; however, Lake Monticello was sampled a second time in 2021 following the results of genetic analysis for the broodstock collection. For the most part, genetic samples were collected from a subset of fish encountered during standard collection protocols described for the CPE analyses, but in some cases, sampling was conducted to collect the specified sample size in the shortest amount of time.

Catch per effort and creel analyses.— Mean CPE of each species was calculated for each sample year in each reservoir and was plotted against year to display temporal trends in Largemouth Bass, Alabama Bass, and overall black bass relative abundance before, during, and after the introduction of Alabama Bass. To better quantify changes in black bass relative abundance, the time series in each reservoir was divided into two time periods based on the approximate timing of Alabama Bass introduction (Table 1). The preintroduction period was defined as samples taken prior to the first collection of Alabama Bass. For reservoirs that were not sampled prior to Alabama Bass introduction (i.e., Parksville Reservoir and Moss Lake), the first three samples taken were considered to be in the “preintroduction” category, as the species was still found in low relative abundance. All other samples were considered to be in the postintroduction period. The one exception to this was Blue Ridge Lake, where Alabama Bass were first captured in gill-net samples in 1993 but did not occur in electrofishing samples until 1999 and remained at low relative abundance levels until the mid-2000s, coinciding with introduction of Blueback Herring *Alosa aestivalis* around 2004 (J. Damer, unpublished data). Therefore, in this case the preintroduction period was considered to be prior to the rapid expansion of Alabama Bass that began in 2006. These time periods in all reservoirs were confirmed through visual inspection of Alabama Bass time series data and in consultation with the biologist that managed each reservoir. Overall CPE for each period was calculated for Largemouth Bass, Alabama Bass, and all black bass and was compared between periods within each reservoir using either a standard ANOVA or a split-plot repeated-measures ANOVA, depending on whether or not the sampling sites were fixed (Maceina et al. 1994; Hubert and Fabrizio 2007; SAS Institute 2012). Likewise, mean CPEs of Largemouth Bass and Alabama Bass during the postinvasion period were compared using ANOVAs as described above.

Creel data were analyzed using programs developed by KGN Consulting, Inc., with methods by Malvestuto et al. (1978) to estimate the total harvest of Largemouth Bass, Alabama Bass, and all black bass for each year (SAS Institute 2012). Only harvest data were available for the creel surveys (i.e., anglers were not queried about how many fish of each species were caught and released) due to concerns about the ability of anglers to correct identify black bass species (Lewis et al. 2021). National trends demonstrate that angler harvest of black bass has declined through time (Allen et al. 2008; Myers et al. 2008), but we assumed that (1) anglers would not preferentially harvest one species relative to another, and thus, (2) harvest would approximately reflect population trends. Sample probabilities for day, time, and strata were used to expand survey data to entire reservoir and year totals. Annual harvests of Largemouth Bass, Alabama Bass, and all black bass combined were plotted against time to examine seasonal trends.

Genetic analyses.— Genetic samples from Tennessee, North Carolina, and Virginia were sent to the Southeastern Fish Genetics Cooperative Lab at Auburn University (Auburn, Alabama). Fish from Lake Monticello, South Carolina, were processed at the Hollings Marine Laboratory (Charleston, South Carolina) in the SCDNR Population Genetics Laboratory. Samples at Auburn University were assessed using single-nucleotide polymorphism markers; South Carolina samples were processed using 16 microsatellite markers developed by SCDNR using a reference set from known species. Detailed methods for both processes are provided in Supplement 1 (available in the online version of this article).

All genetic data were analyzed using STRUCTURE version 2.3.4 (Pritchard and Donnelly 2000). Fish with individual membership coefficients (Q) of 0.95 or greater were assigned to a single species (i.e., “pure”). For hybrid individuals, a Q-value threshold of at least 0.05 for a species was required to be considered a contributing ancestry proportion (Lutz-Carrillo et al. 2006). Species calls from STRUCTURE were used to assign fish to either a pure species or a number of hybrid mixes, and the results were summarized for each reservoir. Hybrid individuals were assigned into two categories: (1) hybrids involving Alabama Bass ancestry using the Q-value threshold described above and (2) all other hybrids.

RESULTS

Trends in Abundance and Harvest

Alabama Bass CPE in Blue Ridge Lake remained low until the mid-2000s, rapidly increasing thereafter to a peak in 2017, with a subsequent decline (Figure 2). Largemouth Bass relative abundance peaked in 2006–2007 and then declined as Alabama Bass CPE increased, eventually leveling out at an annual mean of around 10 fish/h. Comparing the pre-/early Alabama Bass introduction period (1991–2005) to the postintroduction period (2006–2021), the mean CPE of Alabama Bass increased almost 40-fold ($F_{1,4} = 245.86$, $P < 0.0001$), whereas the Largemouth Bass and total black bass CPEs doubled ($F_{1,13} = 11.85$,

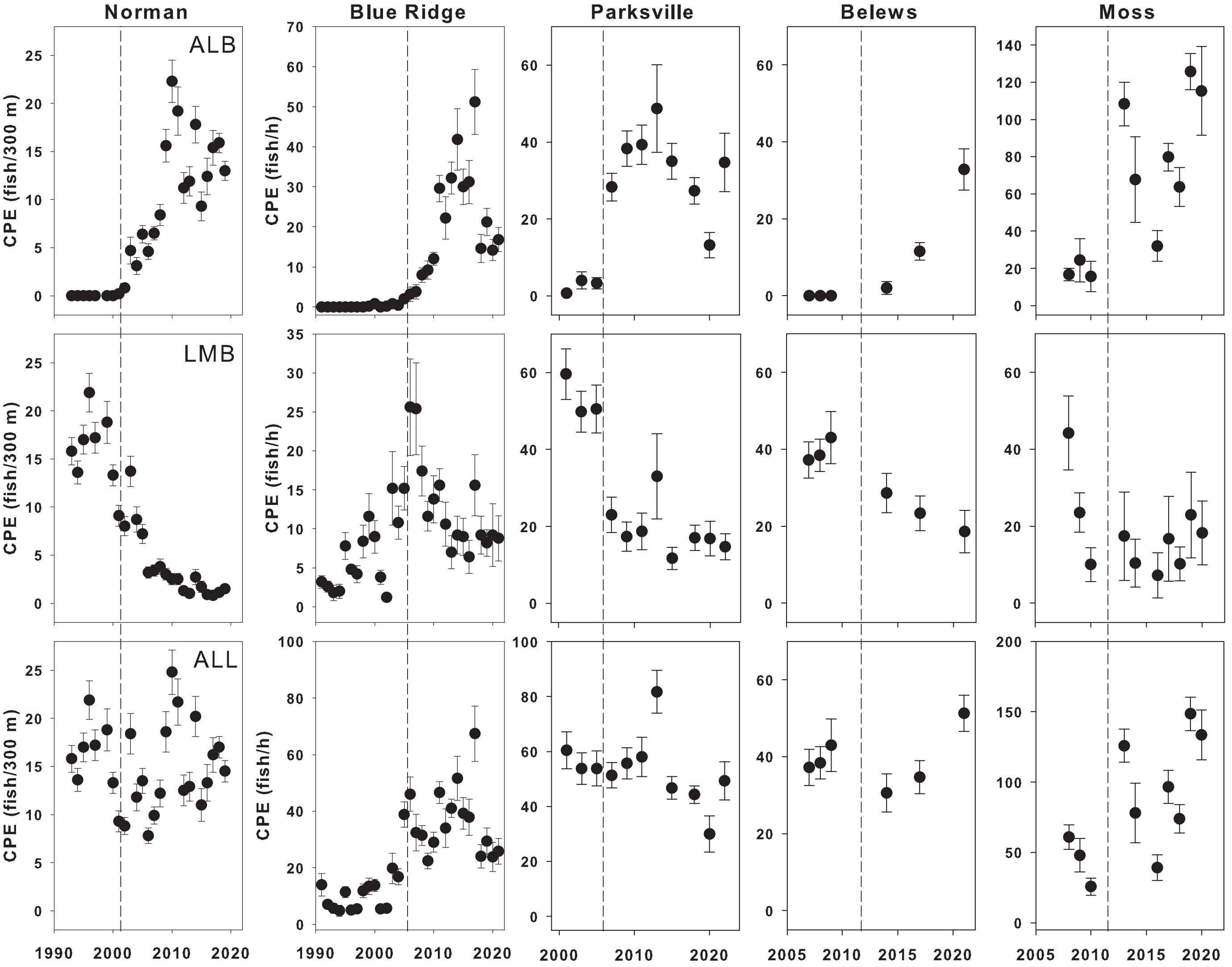

FIGURE 2. Annual mean catch per effort (CPE; fish/300 m of shoreline for Lake Norman; fish/h for all other reservoirs) of Alabama Bass (ALB), Largemouth Bass (LMB), and total black bass (ALL) from spring electrofishing samples in five southeastern U.S. reservoirs. Error bars represent ±SE. Dotted lines separate periods with few or no ALB from those with established ALB populations.

P = 0.0044) and tripled ($F_{1,13}$ = 99.29, $P < 0.0001$), respectively (Table 2). Mean CPEs of Alabama Bass and Largemouth Bass in the postintroduction period were 20.2 and 12.8 fish/h, respectively, but the difference was not significant ($F_{1,16}$ = 0.95, P = 0.3442).

In Lake Norman, the CPE of Alabama Bass increased rapidly after their introduction in 2001, peaking in 2010 (Figure 2). Unlike Blue Ridge Lake, Largemouth Bass CPE in Lake Norman quickly declined after Alabama Bass introduction, whereas total black bass CPE showed no recognizable temporal trends. The mean CPE of Largemouth Bass declined by 77% from before (1993–2000) to after (2001–2019) Alabama Bass introduction ($F_{1,817}$ = 541.82, $P < 0.0001$), but total black bass CPE declined by only 13% ($F_{1,809}$ = 10.67, P = 0.0011; Table 2). The Alabama Bass mean CPE was almost threefold higher than the Largemouth Bass CPE during the postintroduction period ($F_{1,1,218}$ = 259.37, $P < 0.0001$).

Alabama Bass were also first found in Parksville Reservoir during 2001. Relative abundance of Alabama Bass rapidly increased, with a concomitant decline of Largemouth Bass CPE (Figure 2). Alabama Bass CPE in Parksville Reservoir peaked in 2013 at 49 fish/h and then declined. Unlike in Lake Norman, after its initial decline, the Largemouth Bass CPE leveled out at around 15–18 fish/h and showed no sign of further decrease. Total black bass CPE showed a general decline throughout the sampling period (Figure 2). The mean CPE of Alabama Bass increased by more than an order of magnitude between the early introduction period (2001–2005) and the

TABLE 2. Mean catch per effort (SE in parentheses) and percent change for Alabama Bass (ALB), Largemouth Bass (LMB), and total black bass (TOTAL) from spring electrofishing samples in five southern U.S. reservoirs before and after the introduction of nonnative ALB. Means are expressed as fish per hour for all reservoirs except Lake Norman, for which CPE is fish per 300 m of shoreline. For a given reservoir, pre- and postintroduction means with the same letter are not significantly different (least-significant-difference test: $P > 0.05$).

Reservoir	Species	Preintroduction	Postintroduction	Percent change
Belews Lake	ALB	0 (0) y	16.6 (2.7) z	–
	LMB	39.6 (3.0) z	23.0 (3.0) y	−42
	TOTAL	39.6 (3.0) z	39.6 (2.7) z	0
Blue Ridge Lake	ALB	0.5 (0.2) y	20.2 (1.4) z	+3,940
	LMB	6.2 (0.6) y	12.8 (0.9) z	+107
	TOTAL	10.0 (0.8) y	36.5 (1.6) z	+265
Moss Lake	ALB	18.9 (4.6) y	84.6 (7.4) z	+348
	LMB	25.9 (5.2) z	14.7 (3.1) y	−43
	TOTAL	44.8 (6.3) y	99.3 (7.8) z	+122
Lake Norman	ALB	0.0 (0) y	10.8 (0.4) z	–
	LMB	16.8 (0.6) z	3.8 (0.2) y	−77
	TOTAL	16.8 (0.6) z	14.6 (0.4) y	−13
Parksville Reservoir	ALB	2.7 (0.9) y	33.5 (2.3) z	+1,137
	LMB	53.3 (3.5) z	19.2 (2.0) y	−63
	TOTAL	56.0 (3.6) z	52.6 (2.5) z	−5

postintroduction period (2006–2022; $F_{1,125} = 178.52$, $P < 0.0001$), whereas the Largemouth Bass CPE declined by almost two-thirds ($F_{1,125} = 45.28$, $P < 0.0001$); however, total black bass CPE did not change ($F_{1,125} = 1.03$, $P = 0.3114$; Table 2). After establishment, the mean CPE of Alabama Bass was 70% greater than that of Largemouth Bass ($F_{1,186} = 24.49$, $P < 0.0001$).

Belews and Moss lakes, North Carolina, were sampled over shorter time periods than the other three reservoirs, and Alabama Bass introduction in both was also more recent. Alabama Bass CPE in Moss Lake remained low for 3 years before rapidly increasing (Figure 2). Largemouth Bass CPE was over 40 fish/h in the first sample but thereafter ranged from 10 to 20 fish/h in most subsequent years, and no obvious trend was observed. Conversely, total black bass CPE appeared to increase through time (Figure 2). The mean CPE of Alabama Bass increased more than threefold between the early introduction period (2008–2011) and the postintroduction period (2012–2020; $F_{1,2} = 118.99$, $P = 0.0083$), whereas the Largemouth Bass CPE declined by 43% ($F_{1,2} = 57.60$, $P = 0.0169$) and the total black bass CPE doubled ($F_{1,2} = 17.83$, $P = 0.0418$; Table 2). After Alabama Bass establishment, the mean CPE of Largemouth Bass was less than one-third of the Alabama Bass CPE ($F_{1,6} = 1{,}015.08$, $P < 0.0001$; Table 2).

After the introduction of Alabama Bass in 2011, Belews Lake followed a pattern similar to that described above, with Largemouth Bass CPE rapidly declining as Alabama Bass CPE increased (Figure 2). Total black bass CPE displayed no obvious temporal trends during this time, although the last sample (2021) displayed the highest CPE values observed during the study. The mean CPE of Largemouth Bass declined by 42% from the preintroduction period (2007–2009) to the postintroduction period (2014–2021; $F_{1,93} = 18.18$, $P < 0.0001$), and total black bass CPE was essentially identical between periods ($F_{1,92} = 0.11$, $P = 0.7390$; Table 2). Largemouth Bass mean CPE was 28% higher than Alabama Bass CPE during the postintroduction period ($F_{1,110} = 9.07$, $P = 0.0032$; Table 2).

Creel data for Lakes Keowee and Russell showed similar temporal trends after the establishment of Alabama Bass (Figure 3). Harvest of Largemouth Bass declined as Alabama Bass harvest increased in both reservoirs. However, no temporal trend was apparent for total black bass harvest in Lake Keowee, whereas in Lake Russell that metric declined through time, similar to the Largemouth Bass harvest. In Lake Keowee, estimated annual harvest of Largemouth Bass declined below 10,000 fish after 2000, but the harvest of Alabama Bass was more than 20,000 fish annually for all but 2 years after 2000 (Figure 3). In contrast, estimated harvests of Largemouth Bass and Alabama Bass in Lake Russell were more similar to each other except during the final 3 years of sampling (2015–2017), when the harvest of Alabama Bass was 4–10-fold higher than the Largemouth Bass harvest.

Genetic Composition

Genetic surveys of black bass in nine reservoirs within Tennessee, North Carolina, South Carolina, and Virginia found varying levels of Alabama Bass genes (Table 3). Pure Alabama Bass were found in five reservoirs, whereas

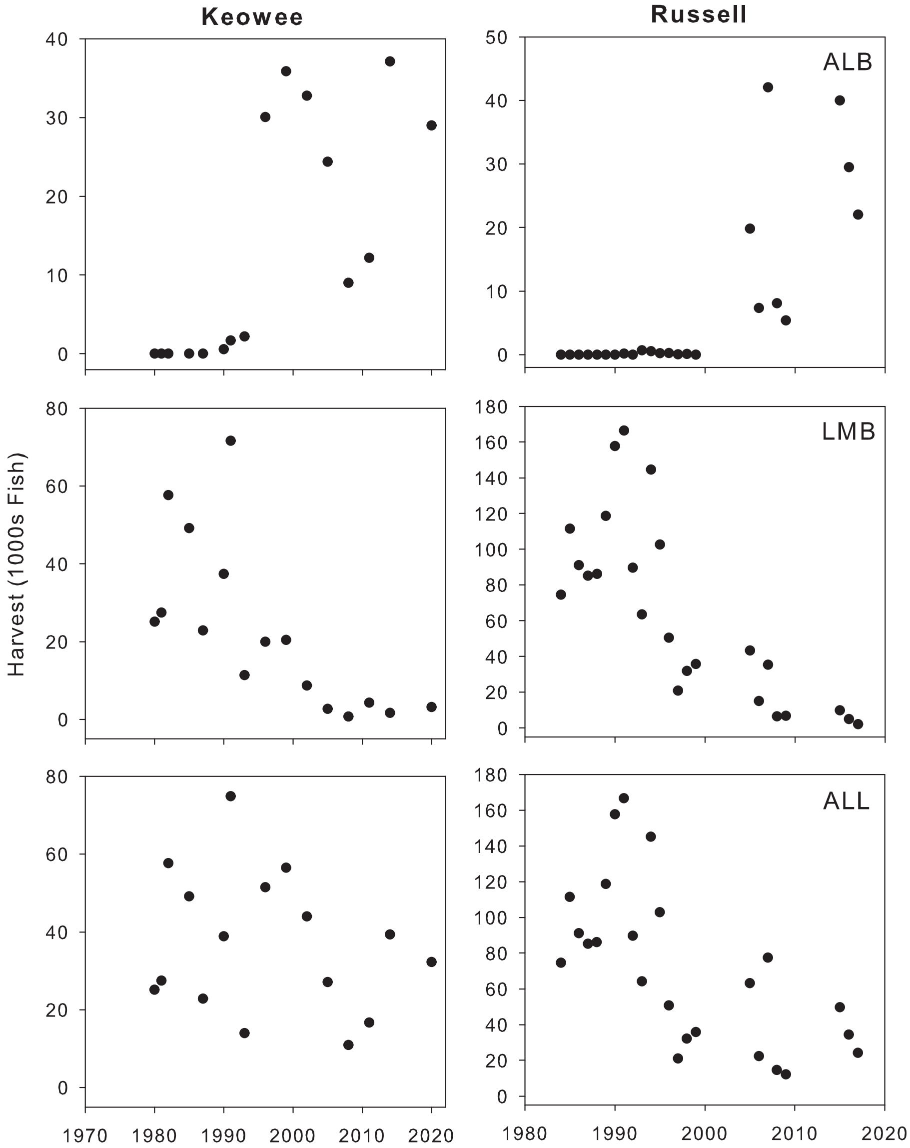

FIGURE 3. Annual estimated harvest of Alabama Bass (ALB), Largemouth Bass (LMB), and total black bass (ALL) from two southeastern U.S. reservoirs. Note the different *y*-axis scales.

all reservoirs had some level of Alabama Bass introgression with other black bass species. In contrast, hybrids between Spotted Bass and other black bass species in these reservoirs were much less common (Table 3). Alabama Bass or their hybrids comprised 50% or more of the black bass sample in five of the nine reservoirs. A Smallmouth Bass broodstock collection in Lake Monticello was found to contain more than one-third hybrids, most of which were hybrids with Alabama Bass (Table 3). A subsequent sample of black bass (excluding Largemouth Bass) was dominated by hybrids. Among all reservoirs, pure specimens of non-Alabama Bass species composed <50% of the sample in six of the nine reservoirs (Table 3).

DISCUSSION

Results of this study demonstrate that Alabama Bass introduction leads to large-scale impacts on existing black bass populations in reservoirs of various sizes. These changes occurred over relatively short time intervals—often within 10 years after detection of Alabama Bass. In many instances, these changes occurred so rapidly that effective control or eradication measures could not have been implemented in time to mitigate the impact, even if such measures had already been designed and ready (Hulme 2006; Vander Zanden and Olden 2008; Britton et al. 2011; Cucherousset and Olden 2011). Once established, these reservoirs then became sources for new

TABLE 3. Genetic results using single-nucleotide polymorphism analysis with species calls from STRUCTURE version 2.3.4. Samples were collected from nine reservoirs in four states. The state where each reservoir is located is indicated in parentheses. Lake Monticello was sampled twice: once for Smallmouth Bass (SMB) broodstock collection (BS) and a second time for a general non-Largemouth Bass (non-LMB) survey. “Target” indicates the objective of each sample. Also presented are the sample size (*N*) and the percentages of fish that were categorized as pure (membership coefficient $Q \geq 0.95$) Alabama Bass (ALB), Largemouth Bass (LMB), SMB, and Spotted Bass (SPB); hybrids with significant ($Q > 0.05$) ALB genes (ALB HYB); and other (non-ALB) hybrids (OTH HYB).

			Species calls in STRUCTURE					
Reservoir	Target	*N*	ALB	LMB	SMB	SPB	ALB HYB	OTH HYB
Claytor Lake (VA)	Non-LMB	192	1.04	2.08	8.33	57.81	29.69	1.04
Diascund Creek Reservoir (VA)	SPB	45	77.78	13.33	–	–	8.89	–
Fontana Reservoir (NC)	SMB	50	–	–	24.00	–	76.00	–
Lake Gaston (NC/VA)	SPB	49	28.57	4.08	–	–	67.34	–
Lake James (NC)	SMB	49	–	–	65.31	–	34.69	–
Lake Monticello BS (SC)	SMB	109	–	–	62.31	–	28.44	9.17
Lake Monticello (SC)	Non-LMB	25	–	–	28.00	–	48.00	24.00
Moss Lake (NC)	SPB	49	95.92	2.04	–	–	2.04	–
Norris Reservoir (TN)	SPB	50	–	–	–	94.00	4.00	2.00
Philpott Lake (VA)	Non-LMB	95	46.32	–	29.47	–	23.15	1.05

secondary introductions into nearby water bodies (Vander Zanden and Olden 2008; Pfauserová et al. 2021). Secondary introductions had already been demonstrated for Alabama Bass, as initial introductions into Lake Lanier and other north Georgia reservoirs in the 1980s (Pierce and Van Den Avyle 1997) spread to reservoirs in the adjacent Savannah River basin within 10 years (Barwick et al. 2006). Thereafter, Alabama Bass spread to Lake Norman and Parksville Reservoir in the early 2000s, then northward and westward to numerous other reservoirs in western North Carolina (Dorsey and Abney 2016; C. S. Loftis, unpublished data). The current leading edge of the Alabama Bass invasion lies in south-central Virginia, where they were discovered in five reservoirs and three river systems between 2018 and 2021 (Virginia Department of Wildlife Resources, unpublished data).

Introduction of nonnative species has long been recognized as a leading cause of biodiversity loss across the globe (Ricciardi and Rasmussen 1998; Gido and Brown 1999; Hulme 2006; Ellender et al. 2014). However, outside of salmonids in the western United States, most of the impacts that have been examined or theorized to occur are focused on nongame species, which are often threatened by the introduction of nonnative piscivores (Whittier and Kincaid 1999; Cambray 2003; Trumpickas et al. 2011). Until recently, black bass have rarely been a part of the IAS issue other than as one of the principal nonnative species causing declines in native species (Whittier and Kincaid 1999; Moyle et al. 2003; Ellender et al. 2014). Because black bass are consistently among the most sought-after sport fish in North America (Shaw 2015), they have been commonly introduced into new water bodies around the world, first by agencies and then by anglers (Jackson 2002; Long et al. 2015; Davis and Darling 2017; Peoples and Midway 2018). Along with impacts on native fish communities, black bass introductions have also been documented to negatively affect native congeners. Guadalupe Bass *M. treculii* in Texas suffered severe declines after the introduction of nonnative Smallmouth Bass (Garrett et al. 2015). Smallmouth Bass were extirpated from several north Georgia reservoirs after introductions of “Spotted Bass” that were subsequently identified as Alabama Bass (Pierce and Van Den Avyle 1997). Bartram's Bass suffered similar declines after the introduction of Alabama Bass into South Carolina reservoirs (Barwick et al. 2006; Bangs et al. 2018). Shoal Bass *M. cataractae* in Alabama streams were found to have been replaced by Spotted Bass × Alabama Bass hybrids over a 40-year period (Stormer and Maceina 2008; S. M. Sammons, unpublished data). Collectively, these examples demonstrate that most impacts of nonnative black bass on native congeners have involved a more widespread species reducing or eliminating more range-restricted endemics that are known to be more vulnerable (Gido and Brown 1999; Perry et al. 2002; Bangs et al. 2018). However, the results of our study demonstrate that Alabama Bass are also capable of impacting Largemouth Bass, the most widely distributed black bass species.

Perry et al. (2002) postulated that threats posed to biodiversity by movement of regional endemics within North America could equal or exceed the threats from outside the continent. Fishes that are moved within a continent represent dual threats to native species: competition (similar to threats posed by intercontinental transplants) and the added threat of introgressive hybridization (Rhymer and Simberloff 1996). Alabama Bass appear to support this theory, as they clearly have some advantage over Largemouth Bass in reservoirs and can rapidly replace them. At the same time, Alabama Bass readily hybridize with other congeners, resulting in loss of genetic integrity or even extirpation of those species (Pierce and Van Den Avyle 1997; Barwick et al. 2006; Leitner et al. 2015; Bangs et al. 2018). Conversely, our data suggested that Alabama Bass rarely hybridize with Largemouth Bass, similar to what Bangs et al. (2018) found in four Savannah River reservoirs within Georgia and South Carolina. It is also possible that both competitive exclusion and introgressive hybridization are occurring simultaneously between Alabama Bass and non-Largemouth Bass congeners, thereby increasing the rate of species loss in these reservoirs (Avise et al. 1997). Unfortunately, once Alabama Bass are established, their impacts are not confined to reservoir fish populations, as they are known to disperse up tributaries and impact native black bass in adjacent systems as well (Sammons and Maceina 2009; Leitner et al. 2015; Peoples et al. 2021; B. Bowen, Georgia Department of Natural Resources, unpublished data). Furthermore, reservoirs function as a convenient introduction point for nonnative fish due to abundant and easy access compared to rivers and streams and are a source and refuge for nonnative species, facilitating their dispersal across the landscape (Peoples et al. 2021; Pfauserová et al. 2021).

The rapid loss of Largemouth Bass from the study reservoirs after Alabama Bass introduction is alarming; however, introgression and formation of hybrid swarms with other black bass species ultimately may have the greatest lasting impact on reservoir fisheries. Hybridization between native and nonnative species can reduce reproductive efficiency, result in hybrid vigor, replace parental species, and reduce genetic integrity (Rhymer and Simberloff 1996; Cucherousset and Olden 2011). Black bass are already known to have weak reproductive isolation barriers (Koppelman 2015; Bangs et al. 2018), and this is likely exacerbated in altered systems, such as reservoirs (Rhymer and Simberloff 1996). Much of the previous work on genetic swamping from nonnative black bass has examined impacts on restricted-range endemics (Pipas and Bulow 1998; Barwick et al. 2006; Leitner et al. 2015; Tringali et al. 2015), but the results of our study suggest that Smallmouth Bass populations may be equally at risk of severe declines or extirpation due to introgression with nonnative Alabama Bass. Unlike Largemouth Bass, Smallmouth Bass have habitat preferences and requirements similar to those of Alabama Bass in lotic and lentic waters (Brewer and Orth 2015; Rider and Maceina 2015); thus, few if any refuges would be available to them once Alabama Bass become established in a system.

Vander Zanden and Olden (2008) noted that the first stage of biological invasions is the invader's arrival to new habitats. Pathways to invasion have been a topic examined by numerous researchers, particularly in the context of predicting the invasion potential of various species (Ricciardi and Rasmussen 1998; Liu et al. 2017; Peoples and Midway 2018). However, motivations and pathways for the introduction of popular and regionally important sport fish species (e.g., Alabama Bass) outside of their native ranges are more obvious, as propagule pressure is primarily determined by the species' popularity with anglers (Davis and Darling 2017). The focus of black bass angling in reservoirs has shifted from family-oriented and harvest-minded endeavors to more solo, competition-driven escapes from everyday life (Schramm and Gerard 2004; Driscoll et al. 2013). Comments offered to fisheries biologists and posts in online forums indicate that anglers consider Alabama Bass to be easier to catch in reservoirs than many congeners due to a perceived tendency to aggregate and greater aggressiveness. In addition, as reservoirs age and as shoreline cover declines, these systems become more suitable for Alabama Bass and less so for Largemouth Bass (Rider and Maceina 2015); thus, Alabama Bass are seen by anglers as a viable supplement to the black bass community. Great advances have been made in technology designed to keep fish alive during competitive tournaments (Schramm and Gilliland 2015), and an unintended consequence of this is likely an enhanced ability to retain and move fish across longer distances than previously possible. In 2008, bass club anglers divulged to a North Carolina Wildlife Resources Commission (NCWRC) biologist that their club had translocated many Alabama Bass from Lake Norman to nearby Moss Lake after a tournament in 2006 (D. Goodfred, NCWRC, personal communication). Uncorroborated stories about similar unauthorized transfers circulate among angler groups and online forums, indicating that this is a pervasive problem that is likely to increase in the future.

The second stage of biological invasions noted by Vander Zanden and Olden (2008) is whether or not an introduction succeeds. Alabama Bass that are introduced into a new system appear to be unusually adept at rapidly colonizing novel habitats. Data in our study showed repeatedly that Alabama Bass abundance rapidly increased over a very short duration. Although the Blue Ridge Lake data suggested that the introduction of another nonnative species (Blueback Herring in this case) can mediate the effects of Alabama Bass on Largemouth Bass, Blueback Herring are also found in Lake Norman, where the largest decline of Largemouth Bass was observed. Most of the reservoirs where we observed a rapid increase in Alabama Bass at the expense of native congeners contain nonnative Blueback Herring or Alewife *A. pseudoharengus*, both of which are coolwater, pelagic zooplanktivores that commonly reach larger sizes than native shads *Dorosoma* spp. (Ney 1981; Kohler and Ney 1982; Bart et al. 2021). Anglers believe that Alabama Bass commonly move offshore and consume Blueback Herring in reservoirs where they coexist, and simulations suggest that diet switching from *Dorosoma* spp. to Blueback Herring would increase the growth of Alabama Bass more than Largemouth Bass (Bart et al. 2021). However, this topic deserves further study.

Bangs et al. (2018) used genetic analyses to determine that replacement of Bartram's Bass by Alabama Bass in four Savannah River reservoirs in Georgia and South Carolina was not attributable to multiple introductions but rather was due to repeated selection of Alabama Bass genes by hybrids backcrossing with pure Bartram's Bass. These results suggest that it likely takes relatively few individuals for Alabama Bass to successfully establish themselves and begin impacting native congeners. Further analyses by Bangs et al. (2018) showed that 10–20 years after Alabama Bass introduction, the black bass community consisted of many hybrid individuals and few pure fish, thereafter transitioning to fewer hybrids and more pure Alabama Bass as the native genomes were eliminated from the systems. Our data suggest that similar processes may be affecting Smallmouth Bass in our study reservoirs.

Much of the emphasis on IAS has been on species from other continents being introduced into North America, such as various species of invasive carp (specifically, bigheaded carp *Hypophthalmichthys* spp.) and snakeheads (Channidae). However, intracontinental introductions of fish can have similar or greater impacts and are much more common. Estimates suggest that more than 65% of nonnative fishes in North America have been spread from other regions across the continent (Perry et al. 2002). Despite the large amount of effort, money, and attention focused on the potential impacts of invasive carp and snakeheads on native fishes, the realized impacts from these introduced fishes, particularly on sport fishes, have been far less than the impacts observed in this study resulting from Alabama Bass introductions over the past two decades (Isel and Odenkirk 2019; Chick et al. 2020; Wood 2020). This is likely due to the additional threat of introgressive hybridization posed by Alabama Bass to native congeners, along with the competitive exclusion threat posed by all nonnative invaders, as theorized by Perry et al. (2002). Thus, biologists and management agencies should broaden their focus away from just a few sensational IAS that garner national attention and should realize that sometimes, the worst invaders can be found in our own backyards.

Management Implications

Freshwater IAS are a growing management concern across North America, and management agencies are struggling to develop effective strategies to prevent, control, and/or eradicate these species before they cause irreparable harm to native fish communities (Cambray 2003; Hulme 2006; Vander Zanden and Olden 2008). Alabama Bass introductions pose a clear and present danger to reservoir black bass fisheries as well as associated populations in lotic systems. The present results demonstrate that these introductions will almost certainly cause rapid declines of all congeners via competitive exclusion, introgressive hybridization, or both, resulting in Alabama Bass becoming the dominant black bass species in the system. Largemouth Bass will likely be relegated to fringe populations in shallow sections of the reservoir (Dorsey and Abney 2016; Goodfred and Wood, in press; K. Hodges, NCWRC, unpublished data), and all other black bass species are likely to be completely extirpated (Bangs et al. 2018). The rate of Alabama Bass spread across the landscape and the speed of species turnover once Alabama Bass become established are unprecedented in large reservoir systems; often, by the time managers recognize the threat, it is already too late to mitigate. Given this, the best strategy to combat Alabama Bass introduction is to prevent future introductions from occurring (Hulme 2006; Britton et al. 2011; Golebie et al. 2021).

Because the primary driver of new Alabama Bass invasions appears to be anglers, new management strategies must be implemented by agencies to discourage or eliminate angler introductions of Alabama Bass (Cambray 2003; Hulme 2006; Cucherousset and Olden 2011). Outreach programs that are implemented to educate anglers about important issues and that attempt to modify their behavior are often ineffective (Hart and Larson 2014; Kemp et al. 2017; Golebie et al. 2021). Public trust in government agencies and science is at an all-time low, and, in recent years, people have been challenging the existing scientific consensus on a variety of topics, including the effects of IAS on native fauna (Russell and Blackburn 2016; Ricciardi and Ryan 2018). Addressing these challenges and resolving conflicts will require adoption of appropriate approaches from other disciplines, such as the social sciences. Biologists must learn to convey findings more persuasively to the public to effect meaningful changes in behavior (Ricciardi and Ryan 2018). Several studies reported that framing IAS conversations in the context of emphasizing their personal impacts on specific user groups rather than broader social and ecological consequences was more effective at creating changes in behavior and actions (Hart and Larson 2014; Golebie et al. 2021). Many times, anglers are unaware of which species are native or nonnative in the places that they fish; such information is easily conveyed and can help in their decision-making process regarding IAS (Cambray 2003). Based on the rapid expansion of Alabama Bass throughout the Carolinas and into Virginia, it is clear that at least a subset of anglers considers the Alabama Bass to be a desirable addition to these fisheries. Finding a message that resonates with anglers about the threat of Alabama Bass introductions to existing black bass fisheries should be a crucial component of management actions going forward if the spread of Alabama Bass is to be halted. Results of this study should go a long way toward assisting agencies in this endeavor.

Finally, agencies need to adopt a risk management approach to IAS whereby the actions to be implemented are commensurate with the level of risk (Britton et al. 2011). A comprehensive IAS management system should be developed that details items such as control options, the biology of potential IAS, the impacts of IAS on other species (including economic and societal impacts), and educational outreach efforts as described above (Cambray 2003). Legislation should support these programs, including strict regulation of nonnative fish translocation at the state and federal levels and funding for IAS programs, which typically suffer from chronic underfunding that limits their effectiveness (Cambray 2003; Vander Zanden and Olden 2008). Enforcement of regulations that are designed to stop private citizens from introducing nonnative fishes is often difficult, but simply having such regulations in place and well publicized would be sufficient for some people to cease this practice, depending on their existing value and belief systems (Kemp et al. 2017).

Robust sampling designs are also a vital component of detecting invasions as early as possible. Black bass species use habitat in different ways, requiring careful consideration of sampling site selection across several scales to sample multiple species effectively (Buynak et al. 1989; Sammons and Bettoli 1999; Goclowski et al. 2013). The importance of long-term data sets for adequately describing and quantifying ecosystem change cannot be overstated (Bonar et al. 2009). Two of our study reservoirs had no monitoring program in place prior to the arrival of Alabama Bass; thus, “preintroduction” conditions were not described. However, it was possible to demonstrate black bass community change after Alabama Bass introduction in another reservoir even though the reservoir was only sampled every 3 years. Regulatory agencies continue to be stretched for time and effort as budgets shrink and responsibilities multiply, but our results demonstrate that even intermittent sampling of a reservoir is worth the investment and better than not sampling at all. Likewise, regular genetic sampling of black bass populations by using a standardized monitoring program is likely required to adequately describe the impacts of nonnative congeners, particularly in systems where Smallmouth Bass support economically important fisheries.

Hybrids between native and nonnative black bass are often cryptic and difficult to identify in the field (Lewis et al. 2021). Such was the case during the present study, as fish were correctly identified in the field only about two-thirds of the time for reservoirs with high rates of introgression. This is particularly problematic in reservoirs with existing Spotted Bass populations that are subsequently invaded by Alabama Bass. Although the two species can be successfully distinguished using morphometric and meristic characters (Baker et al. 2008), they are not readily discernable if biologists are unaware that Alabama Bass are present, thus lengthening the time between initial introduction and discovery and giving the species more time to establish itself before any remedial actions can be taken. Further, cryptic hybrids can confound broodstock collection for hatcheries, requiring all broodstock to be genetically screened prior to spawning so as to avoid unintentionally spreading nonnative genes into novel areas. Therefore, introductions of Alabama Bass can increase the time, effort, and expenditures associated with routine fisheries operations.

The introduction of Alabama Bass has virtually eliminated Smallmouth Bass populations in many Georgia and North Carolina reservoirs and now threatens numerous others, such as those in Dale Hollow Lake, Tennessee, and the New and James rivers, Virginia. However, the final extent of Alabama Bass invasions is unknown. Little is known about this species' thermal requirements or limitations, early life history, or reproductive needs (Rider and Maceina 2015). Thus, it is hard to predict the limits of Alabama Bass invasions. Famous and economically important Smallmouth Bass fisheries in the Susquehanna River, Pennsylvania, and Lake Erie are currently in the path of the rapid northward movement of Alabama Bass, and the loss of these fisheries would be catastrophic to local economies and anglers. Alabama Bass introduction may constitute the greatest ecological threat to black bass fisheries over the long history of managing these species. Nothing less than an immediate and concerted effort among anglers, managing agencies, scientists, and legislatures will serve to address the multifaceted challenges posed by this issue and halt the spread of Alabama Bass.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.