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CONSERVATION OF ENDEMIC BARTRAM'S BASS: NESTING MICROHABITAT
USE AND SPATIAL DISTRIBUTION WITH CONGENERS IN THE
SAVANNAH RIVER BASIN

A Thesis
Presented to
the Graduate School of
Clemson University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
Wildlife and Fisheries Biology

by
Emily Elizabeth Judson
December 2018

Accepted by:
Dr. Brandon Peoples, Committee Chair
Dr. Troy Farmer
Mrs. Jean Leitner

ABSTRACT

Bartram's Bass *Micropterus sp. cf. cataractae* is endemic to the Savannah River basin of South Carolina and Georgia. Bartram's Bass is threatened by habitat alteration and hybridization with invasive Alabama bass (*M. henshalli*) and other non-native co-occurring congeners. This study aimed to identify reproductive habitat preference of this species, and factors contributing to its occurrence.

In Chapter 1 we identified Bartram's Bass nesting preference throughout the upper portion of its native range. In spring/summer 2017 and 2018, snorkel surveys were performed in tributaries to quantify nesting microhabitat use of Bartram's Bass. Zig-zag transects were used to locate nests and to quantify habitat availability. Nesting microhabitat parameters were recorded at each nest detected, and eggs were collected for genetic analysis. Average velocity at the 39 pure Bartram's Bass nests observed was 0.09 ± 0.02 m/s, SD, lower than average available velocity of 0.22 ± 0.01 m/s, SD ($p=0.0028$). Average depth of nests was 0.70 ± 0.04 m, SD and was similar to those available 0.67 ± 0.02 m, SD ($p=0.6946$). The substrates used in nests during both breeding years combined were primarily silt (36%), cobble (31%), and gravel (21%), whereas the most available substrates observed in transects were bedrock (23%) and cobble (23%) ($P<0.0001$). On average, nests were 1.84 ± 0.25 m from the nearest bank, and 4.67 ± 0.56 m from the nearest upstream flow influence. Differences between available and used habitat metrics indicate that velocity may be more important than depth or substrate when Bartram's bass are selecting nest sites. While there is a relationship between substrate use and availability, we believe the main factor driving

substrate use is velocity and that certain substrate types are likely a byproduct of selection for velocity.

In Chapter 2 we determined the relative importance of abiotic factors and distance from reservoirs for predicting occurrence of Bartram's Bass. From March to November of 2017 and 2018, individuals were collected from 160 sites across the upper Savannah River basin. Sites represented a gradient of key abiotic variables—watershed- and riparian-scale land use types, ecoregions, stream gradient, and elevation. Genetic analysis of 241 individuals from 50 sites revealed Bartram's Bass were present at 33 sites, and hybrids were present at 21 sites. Conditional inference trees were used to predict the variables that drive Bartram's Bass distribution. Forested land cover at the watershed scale was the most significant predictor of Bartram's Bass presence ($p=0.0236$). Pure individuals preferred sites of greater than 75% forested cover ($p<0.001$). In less forested watersheds, there was higher probability of finding pure Bartram's Bass at sites with greater watershed areas ($p<0.001$), and increased distance from reservoirs ($p<0.001$). Even when forested land cover was greater than 75% and stream gradients were low, sites closer to reservoirs were less likely to harbor pure fish ($p<0.001$). These results reflect the tradeoff between land cover and distribution for facilitating spread and hybridization of invasive fishes.

DEDICATION

I dedicate this thesis to the memory of my grandfather, Thomas Edward Judson, who passed away while I was completing this degree (3/19/1924- 2/11/2017). A farmer, hunter, angler, trapper, and lover of all things outdoors- I can only hope to live a life as full as his. I know this work would have made him proud.

I also dedicate this to my mother and father, Karen Hansen and Doug Judson, for instilling in me a passion for hard work, and for the outdoors; I would not be where I am today had it not been for your love and constant encouragement over the years.

ACKNOWLEDGMENTS

Thank you foremost to my advisor Dr. Brandon Peoples for accepting me as one of your first Master's students, and for providing me the opportunity to study an amazing species. This research has challenged me in ways I never thought possible, and allowed me to learn and grow in ways I didn't know I needed to. I appreciate your patience and tactful support throughout the research and writing process. Thanks to my committee for their support and guidance, Dr. Troy Farmer and Mrs. Jean Leitner. Thank you to all who made this research possible, especially those who provided funding. I am forever grateful for the assistance of my field technicians: Jon Blalock, Alex Michaeli, Wesley Moore, and Luke Bell, as well as the many undergraduates who helped with lab work through Creative Inquiry courses. Thank you to my fellow graduate students, Sam Silknetter, Josh Vine, and Lauren Stoczynski for providing support and laughs through what might have otherwise been stressful times. Immense thanks also to Matt Walker, Tanya Darden, and Kimberly Kanapeckas from the South Carolina Department of Natural Resources (SCDNR) Hollings Marine Lab in Charleston, SC for processing all of my samples. The Clemson office of SCDNR also provided enormous field assistance which I am grateful for, and I would especially like to thank Mark Scott, Kevin Kubach, Drew Gelder, and Kenson Kanczuzewski for all the time and effort you put into my research.

Finally, thank you to my siblings, parents, and grandparents- for shaping me into who I am, loving and supporting me, and inspiring me to pursue my passions relentlessly.

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GENERAL INTRODUCTION

Species can be transported outside their native ranges by deliberate and unintentional introduction (Pyšek and Richardson 2010), natural introduction, or may become invasive within their native ranges (Scott and Helfman 2001). Species transported outside their native range carry several associated risks, and can present difficult management implications in recipient systems (Ricciardi et al. 2013). Nonnative species introductions can have detrimental impacts on native organisms, especially if they become invasive. However, only a fraction of introduced species successfully establish to invade a new system (Williamson and Fitter 1996; Allendorf and Lundquist 2003; Pyšek and Richardson 2010). The success of an invasive species relies on multiple factors, including the habitat and climate of the invaded system (Blackburn et al. 2011), traits of the invasive species (Huxel 1999; Blackburn et al. 2011), and propagule pressure (Catford et al. 2009; Blackburn et al. 2011). When a species is identified as invasive, it has already established a self-sustaining population, and may have already caused damaging impacts on the native ecosystem (Ricciardi et al. 2013). Invasive species pose major threats to biodiversity, ecosystem stability, agriculture, fisheries and public health (Lee 2002). Invasions cause communities to form which were originally absent in the ecosystem, resulting in novel interactions between species that would not have existed otherwise, such as competition between the nonnative and native species and hybridization, which may result in declines in native populations (Huxell 1999).

Hybridization is a major mechanism by which invasive species impact native species (Huxel 1999). Hybridization can occur in any system containing distinct species

capable of reproducing (Rhymer and Simberloff 1996; Huxel 1999), and is common across taxa (Simberloff 1996; Schwartz et al. 2004; Latch et al. 2006). It can occur at localized scales, or broadly over a species' range. Hybridization can cause population decline, extinction, or loss of genetically distinct populations (Alvarez et al. 2015). The most common and detrimental effect of hybridization is the potential loss of the native genetic lineage (Hubbs 1955). Hybridization can cause 'genetic swamping' of native genomes through introgression, often resulting in 'hybrid swarms' in which fertile hybrids displace native parental populations (Anderson 1953). When gene pools intermix, genetic differentiation between parent species can be dissolved, and create higher inheritance of maladapted genes (Huxel 1999; Alvarez et al. 2015; Bolnick 2015). Introgressive hybridization can result in extinction of native species, especially within endemic populations, and its most basic effects consist of erosion and degradation of native genotypes (Rhymer and Simberloff, 1996; Alvarez et al. 2015). Despite the dramatic effects hybridization can have on an ecosystem, the potential for and effects of interbreeding between nonnative and native individuals is an often overlooked impact of species invasions (Huxel 1999).

Ray-finned fishes (Actinopterygii) hybridize more frequently than other vertebrate classes, especially when co-occurring congeners use similar habitats for reproduction (Ryman and Utter 1986; Scribner et al. 2001). Hybridization is widespread among freshwater fishes, being common among many families including Esocidae, Catostomidae, Leuciscidae, Centrarchidae, Salmonidae, and Percidae (Crossman and Buss 1965; Greenfield et al. 1973; Keck and Near 2009; McKelvey et al. 2016).

Hybridization with invasive species poses a threat to many fish populations, especially those that are endemic and have relatively small ranges (Koppelman and Garrett 2002). Although the processes and predictors of invasion have been widely studied in fishes (Moyle and Light 1996; Moyle and Marchetti 2006; Rahel and Olden 2008), still little is known concerning how the mechanism of hybridization impacts the native fish assemblage after an invasion in a system (Avisé et al. 1997; Barwick et al. 2006; Pipas, and Bulow 2011; Peterson 2015).

The black basses (Centrarchidae: *Micropterus*) include some of the most popular sportfishes in the United States, and congruently the most widely introduced species (Jackson 2002; Peoples and Midway 2018). There are currently nine recognized species of black bass in the southern US, including the widely sought after Alabama Bass (*M. henshalli*), Florida Bass (*M. floridanus*), Largemouth Bass (*M. salmoides*), Spotted Bass (*M. punctulatus*), and Smallmouth Bass (*M. dolomieu*), and more narrowly distributed Redeye Bass (*M. coosae*), Shoal Bass (*M. cataractae*), Guadalupe Bass (*M. treculi*), and Suwannee Bass (*M. notius*) (Ramsey 1973; Koppelman and Garrett 2002). However, other taxa have been proposed as distinct species, including the Cahaba Bass (*M. cahabae*), Chattahoochee Bass (*M. chattahoochae*), Choctaw Bass (*M. haiaka*), Tallapoosa Bass (*M. tallapoosae*), Warrior Bass (*M. warriorensis*), Altamaha Bass (*M. sp. Cf M. coosae*), Bartram's Bass (*M. sp. Cf M. cataractae*), and Neosho Smallmouth Bass (*M. dolomieu velox*). Numerous introductions of the more cosmopolitan black basses have led to widespread hybridization and introgression with the rarer black basses (Avisé et al. 1997; Koppelman and Garrett 2002; Barwick et al. 2006; Bangs et al. 2017).

For example, Guadalupe Bass, native to the Edward's Plateau of Texas, has become extirpated in parts of its historical range due to introgression with the nonnative Smallmouth Bass (Whitmore 1983; Littrell et al. 2007), and Shoal Bass are threatened by hybridization with Spotted Bass (Awise et al. 1997; Alvarez et al. 2015).

A species of particular interest is Bartram's Bass, an endemic to the Savannah River basin of South Carolina and Georgia, USA. Individuals have been commonly referred to throughout its range as the Redeye Bass. However, Freeman et al. (2015) identified this species to be more closely related to Shoal Bass, and supported the elevation of Bartram's Bass to species status. The range of Bartram's Bass extends from below the fall line of the mainstem Savannah River to the cool, medium-to-high gradient stream segments typically found above the fall line (Leitner et al. 2015; Oswald et al. 2015). It has been introduced in the Saluda River of the Santee drainage (Bettinger 2015). Bartram's Bass face a multitude of threats including poor land-use practices, and hybridization with congeners, including the Smallmouth Bass and the Alabama Bass (Oswald et al. 2015; Bangs et al. 2017).

Alabama Bass were introduced into the Savannah River basin in the 1980s by anglers to create a local reservoir sport fishery for the species (Oswald 2007). Alabama Bass have since become widespread in the upper Savannah River reservoirs (Bangs et al. 2017), and are now colonizing the tributaries associated with those reservoirs (Leitner et al. 2015). Bartram's Bass populations currently thrive in tributaries, and it is speculated that their populations have been restricted farther upstream since Alabama Bass have

invaded (Oswald et al. 2015). Bartram's Bass and Alabama Bass hybrids have been found in the tributaries; however, it is unknown to what extent hybridization is occurring.

Understanding microhabitat preference is particularly important for native and nonnative congeners that hybridize (Todd and Rabeni 1989; Orth and Newcomb 2002; Perkin et al. 2010). Microhabitat preference can help determine what is enabling two species to hybridize, and thus is an effective indicator of an isolating mechanism as different species occupying the same area may utilize similar water velocities, depths, and substrate (Perkin et al. 2010). Quantifying reproductive microhabitat requirements can serve as a first step toward identifying reproductive isolating mechanisms (Rosenfeld 2003). It will also be useful to identify how future land use changes might impact Bartram's Bass nesting habitat and contribute to further degradation. Although studies assessing other fluvial basses' microhabitat use have been conducted (Saunders et al. 2002; Perkin et al. 2010; Bitz et al. 2015); there is currently no knowledge of Bartram's Bass reproductive preferences. Accordingly, the first objective of this study is to identify the nesting microhabitat selection of Bartram's Bass.

In the case of hybridization with a nonnative species, it is imperative to identify areas for management that may favor the native species (Huxel 1999; Rosenfeld 2003; Perkin et al. 2010). Determining the habitats and environmental factors that best predict Bartram's Bass presence will be vital in managing habitat for the Bartram's Bass in the future. Accordingly, the second objective of this study is to assess the spatial patterns of hybridization between Bartram's Bass and invasive Alabama Bass.

CHAPTER ONE

NESTING MICROHABITAT CHARACTERISTICS OF BARTRAM'S BASS

Introduction

Fishes require a variety of habitats to meet life history requirements over their lifespan; habitats for key activities such as feeding, spawning, and sheltering vary through space and time (Schlosser 1991; Fausch et al. 2002). Identifying reproductive microhabitat requirements is particularly important, as this activity sets the context for all other life stages (Balon 1975). Understanding spawning microhabitat preferences of fishes allows for prediction of population- (Winemiller 2005) and community-level (Berkman and Rabeni 1987) responses to environmental change, and provides key insight into the conservation and management of imperiled fishes (Johnston 1999; Rosenfeld 2003). This is particularly true for imperiled fishes that are threatened by hybridization with nonnative congeners (Todd and Rabeni 1989; Orth and Newcomb 2002; Perkin et al. 2010). Understanding spawning microhabitat requirements can be the first step toward identifying potential disruption of genetically isolating barriers that facilitate hybridization.

The black basses (Centrarchidae: *Micropterus*) include some of the most popular sportfish species in the United States. Currently, there are nine recognized species of black bass in the southern US (Near et al. 2003, Baker et al. 2013; Tringali et al. 2015), but approximately twenty may actually exist (Tringali et al. 2015). A few species in this genus have large native range sizes, but several others are restricted to single or a few river basins in the southeastern US. Because of their popularity, the black basses are

among the most widely introduced freshwater fish species in the world (Jackson 2002; Peoples and Midway 2018). Due to widespread introductions of some black bass species outside their native ranges, many of the endemic black basses in the southeastern US are threatened by hybridization with cosmopolitan species such as Spotted Bass *M. punctulatus*, Alabama Bass *M. henshalli*, Smallmouth Bass *M. dolomieu*, Florida Bass *M. floridanus*, and Largemouth Bass *M. salmoides* (Awise et al. 1997; Koppelman and Garrett 2002; Barwick et al. 2006; Bangs et al. 2017). Although spawning microhabitats have been quantified for numerous species (Saunders et al. 2002; Dauwalter and Fisher 2007; Strong et al. 2010; Bitz et al. 2015), large gaps remain for many others.

One understudied southeastern species is Bartram's Bass, an endemic of the Savannah River basin of South Carolina and Georgia (Freeman et al. 2015; Leitner et al. 2015; Oswald et al. 2015). Bartram's Bass is threatened by habitat alteration and hybridization with the nonnative congeners Alabama Bass and Smallmouth Bass (Barwick et al. 2006; Oswald et al. 2015; Bangs et al. 2017). Alabama Bass were introduced into the Savannah River basin in the 1980s by anglers to create a local sport fishery for the species (Oswald 2007). Alabama Bass have since become widespread in the upper Savannah River basin, and are now colonizing the tributaries where Bartram's Bass occur (Leitner et al. 2015). Smallmouth Bass were introduced in mainstem of the middle Savannah River near Augusta, GA in the late 1990s, and have been annually stocked in Lake Jocassee by the South Carolina Department of Natural Resources (Bangs et al. 2017) (Figure 1). Identifying spawning microhabitat preference of Bartram's Bass throughout its range will be a critical first step to understanding the mechanisms that

drive its imperilment through hybridization with nonnative congeners. Accordingly, the objective of this study was to quantify the spawning microhabitat preferences for key variables (namely depth, flow velocity, and substrate types) of Bartram's Bass in the upper Savannah River.

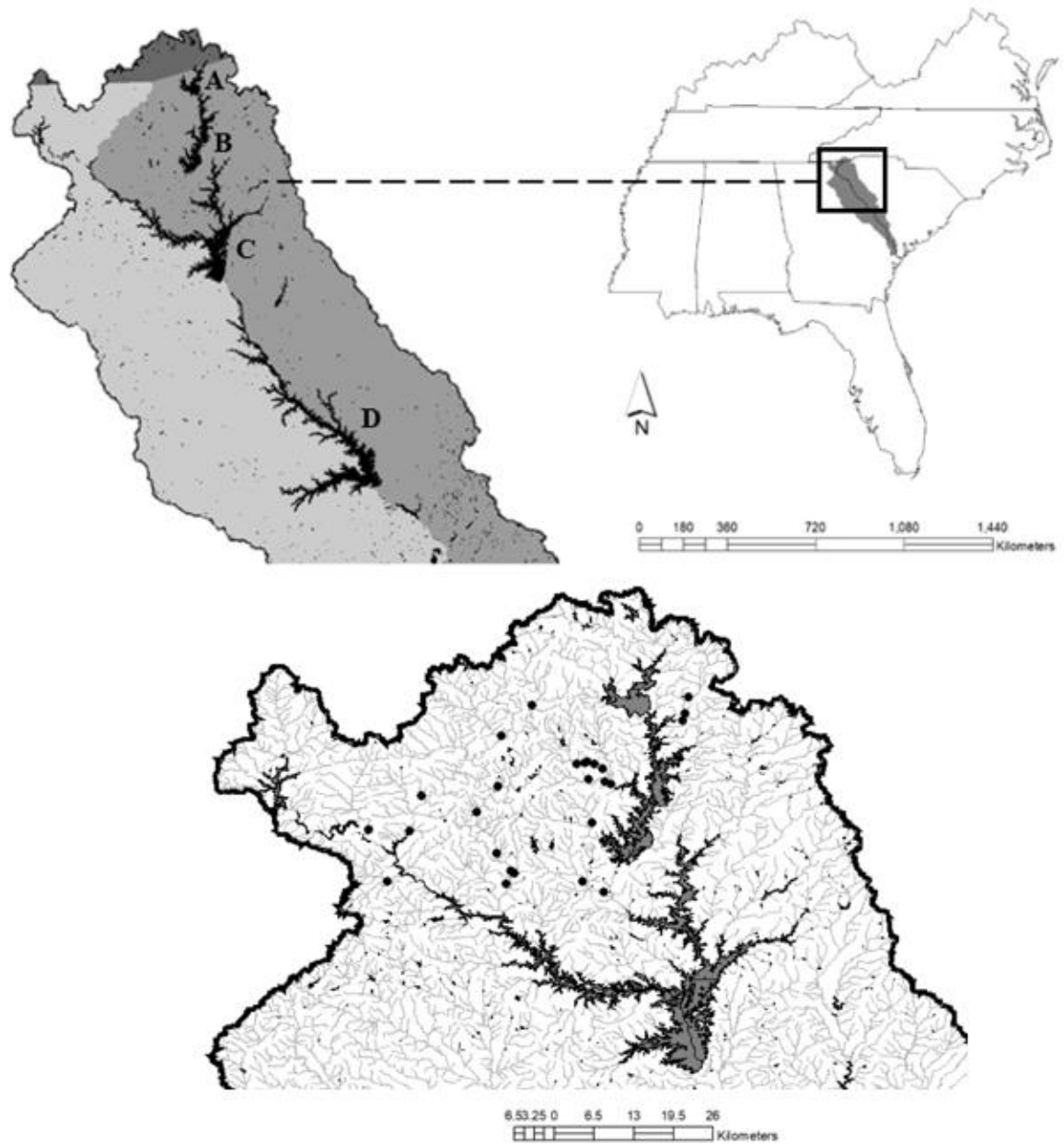


Figure 1. Map of study area (top) and snorkel sites (bottom). Shaded areas of the map on the top left represent different states: North Carolina (dark gray), South Carolina (medium gray, and Georgia (light gray). Reservoirs of the upper Savannah River basin are labeled as letters: Jocassee (A), Keowee (B), Hartwell (C), and Russell (D).

Methods

Study Area

The Savannah River basin spans 27,394 km², and forms the border between the Georgia and South Carolina. It encompasses 15,076 km² in eastern Georgia, 11,865 km² in western South Carolina, and 453 km² in southwestern North Carolina. There are four large impoundments in the upper Savannah River basin: lakes Jocassee, Keowee, Hartwell, and Russell (Figure 1). Land use in the upper Savannah River basin consists of 55.3% forested land, 27.4% agricultural land, 9.3% urban land, 5.7% water cover, 1.7% forested wetland, and 0.6% barren land (DHEC 2017). The upper Savannah River is located in the Southern Blue Ridge Escarpment and upper southern Piedmont ecoregions (Omernik 1987) above the fall line. The Piedmont is heavily impacted by development and urbanization, whereas the uplands of the Blue Ridge that make up the most northern reaches of the Savannah River basin are heavily forested and less impacted (SCDHEC 2017). The inner and outer Piedmont regions make up most of the upper Savannah River watershed (Omernik 1987). Below the fall line, the Savannah flows through the Southeastern Plains and Southern Coastal Plain regions (Omernik 1987). This study included tributaries of the upper Savannah River basin of Georgia and South Carolina, USA.

Field Methods

We surveyed 27 sites (300-m reaches) in upper Savannah River tributaries to quantify bass nesting microhabitat preference (Figure 1). Sites were selected for low turbidity to facilitate snorkeling, considering access constraints. We selected sites across

a gradient of stream size, land use, and distance from impoundments. HOBO temperature loggers were deployed at the downstream and upstream-most sites on each stream. Daily discharge for each stream was obtained from U.S. Geological Survey gauges. Water data was obtained from the USGS 02177000 Chattooga River flow gage near Clayton, GA which was used as a reference site for snorkeling conditions.

Three-person crews surveyed two-to-three sites each day via snorkeling from mid-April to mid-July of 2017 and 2018. Each site was visited at least three times throughout the duration of each season to ensure as many nests were detected as possible. Each time a site was revisited, previous nests found at those sites were examined to ensure we did not sample the same nest twice. Crews worked upstream in a zig-zag pattern to locate nests (Thurrow et al. 2013). A nest was evidenced by a guarding male (Enriquez et al. 2016), or by the detection of eggs scattered on substrate with subsequent observation of a guarding bass. Once a nest was detected, it was marked and georeferenced. Photos and videos were taken to capture nesting activity and behavior of any tending adult males. Workers then returned to finish the transect, and revisited nests to collect eggs and habitat data upon completion of the survey.

Upon returning to a nest, we attempted to capture the guarding adult male off the nest using hook-and-line sampling (Lukas and Orth 1995). The nest was guarded by field crew members during the guarding males' absence. We collected a pectoral fin clip of the parent for genetic analysis, and measured total length (mm) and weight (g) of each fish. Depth (m), velocity (m/s), and ten substrate samples (mm) were then recorded at each nest (Dauwalter and Fisher 2007). We categorized substrate measurements based on a

modified Wentworth scale (Table 1). Nests with eggs broadcasted over detritus (dead organic material) and silt were categorized together in the silt category. Nest widths were measured on axes parallel and perpendicular to flow. We also measured distance (m) from nest location to the nearest upstream flow influence (i.e. boulder or large woody debris), and distance to the nearest bank (m) (Dauwalter and Fisher 2007). At least ten eggs were collected at each nest and preserved in 200-proof ethyl alcohol for genotyping. We measured overall available habitat on transects at each nest location. Some transects applied to multiple nests, if those nests were within 10 m of one another. Depth (m), velocity (m/s), and substrate based on the same categorical scale as nests (Table 1), was measured at ten equidistant points along each transect.

Table 1. Substrate categories and size ranges (mm) as derived from the Wentworth Scale (Wentworth 1922).

Substrate Category	Size of aggregate (mm)
Bedrock	Embedded rock
Boulder	> 256
Cobble	64 - 256
Gravel	2 - 64
Sand	0.06 - 2
Silt	< 0.06

Analyses

Species identities had been developed using molecular tools described by Bangs et.al. (2017). Fin clips and egg samples from nests were processed at the Hollings Marine Laboratory in Charleston, SC in the South Carolina Department of Natural Resources Marine Resources Research Institute. Only nests identified as pure Bartram’s Bass were

included in the following analyses, this determination was based on all 10 analyzed eggs amplifying as pure.

We compared nesting microhabitat variables (depth, velocity, and substrate) to transect data to examine spawning microhabitat specificity, and to identify differences between available and used habitats. Depth and velocity variables were examined for normality, then log-transformed. We used the *lmerTest* package in R version 3.4.3 (R Development Core Team, 2017), to fit linear mixed effects models to identify differences in measurement location (nest vs. transect), nesting season (2017 and 2018), and their interaction for depth and flow velocity, separately. These models contained a random intercept of nest identity to account for non-independence of measurements at nests and paired transects. We used the *multcomp* package to conduct *post hoc* means comparisons in a conservative Tukey's test on velocity for models with significant interactive effects of sample location and spawning year. We used a chi-squared analysis to determine substrate use versus availability within individual breeding seasons and seasons combined.

Results

Nesting activity was observed from 16 May to 13 June in 2017, and from 5 May to 23 June in 2018 when water temperatures were around 20°C. We located 75 nests, 34 at 6 sites in 2017, and 41 nests at 11 sites in 2018. Nests were found within 7 tributaries. Of those, 39 were identified as pure Bartram's Bass; only these were included in analyses.

High water events that created dangerously high water levels and increased turbidity impacted our ability to survey during portions of both the 2017 and 2018 sampling seasons. Between 20 May and 30 May 2017, and 3 June and 10 June 2017, no surveys were conducted due to rain events. These 2017 rain events resulted in discharges greater than 800 cfs for eight consecutive days in May, as recorded at USGS 02177000 Chattooga River flow gage near Clayton, GA, which was used as a reference site for snorkeling conditions. Additionally, for 5 days in the beginning of June discharge was between 400 and 700 cfs. Just two nests were found (on 25 May 2018) between 14 May 2018 and 7 June 2018 due to similar rain events as those that occurred in 2017; 2018 rain events resulted in discharge greater than 1,000 cfs for 23 consecutive days (15 May to 6 June 2018).

We observed Bartram's Bass spawning in pockets comprised of slow water and variable depths close to the banks. Some microhabitats were used for nesting in both 2017 and 2018. However, we cannot determine whether the same individuals were returning to the same area to spawn. Main effects of measurement location show that Bartram's Bass chose significantly lower water velocities for nesting across 2017 and 2018 ($\bar{x} = 0.09 \pm 0.02$ m, SD) than those available ($\bar{x} = 0.22 \pm 0.01$ m, SD) ($p = 0.0028$). The interaction effect between measurement location and year was significant for velocity ($F_{1, 368} = 4.21, p = 0.0408$) (Table 2). A *post hoc* Tukey's test on velocity revealed a significant difference between used and available velocities in 2018 ($p < 0.0001$), and that Bartram's Bass selected for significantly slower velocities for nesting in 2018 ($\bar{x} = 0.01 \pm 0.001$ m/s, SD) than 2017 ($\bar{x} = 0.12 \pm 0.03$ m/s, SD)

($p=0.0304$) (Table 3). The range of available velocities was similar between years (Figure 2).

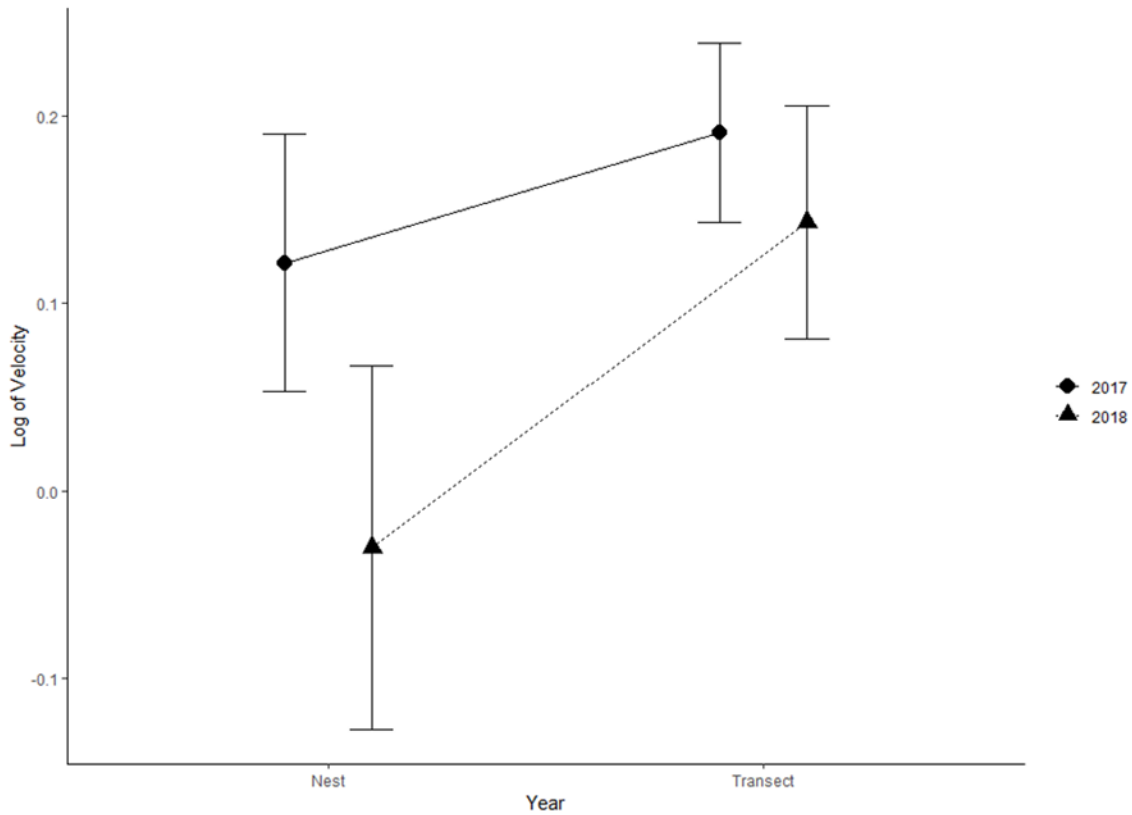


Figure 2. Interaction of used and available velocities among two sampling years (2017 & 2018). Plotted values are least square means (\pm standard error) from ANOVA model.

Table 2. Linear regression model results for water velocity used at Bartram’s Bass nests and available in transects in the upper Savannah River in 2017 and 2018.

Effect	$F_{1, 368}$	p
Transect	23.0	<0.001
Year	6.9	0.0091
Transect: Year	4.2	0.0408

Table 3. Post hoc Tukey’s test on water velocity of nest use and habitat availability in the upper Savannah River in 2017 and 2018.

Effect	Parameter estimate	Std. Error	$Z_{1, 407}$	p
2018 Nest: 2017 Nest	-0.15	0.06	-2.7	0.0304
2017 Transect: 2017 Nest	0.06	0.03	2.4	0.0596
2018 Transect: 2018 Nest	0.17	0.04	4.1	<0.001

Bartram’s Bass did not select for specific water depths for nesting ($\bar{x}= 0.70 \pm 0.04$ m, SD) compared to those available ($\bar{x}= 0.67 \pm 0.02$ m, SD) ($p= 0.6946$), although there was a significant difference in available depth between years ($F_{1, 370}=11.53$, $p=0.0008$) (Table 4). No interaction was found between measurement location and year for depth ($F_{1, 370}=0.19$, $p=0.6635$). On average, Bartram’s Bass utilized shallower depths in 2018 (2017: $\bar{x}= 0.76 \pm 0.04$ m; 2018: $\bar{x}= 0.54 \pm 0.09$ m), but available depths in 2018 ($\bar{x}= 0.76 \pm$

0.03 m) were significantly shallower than those in 2017 ($\bar{x} = 0.46 \pm 0.03$ m; $p=0.0008$) (Figure 3).

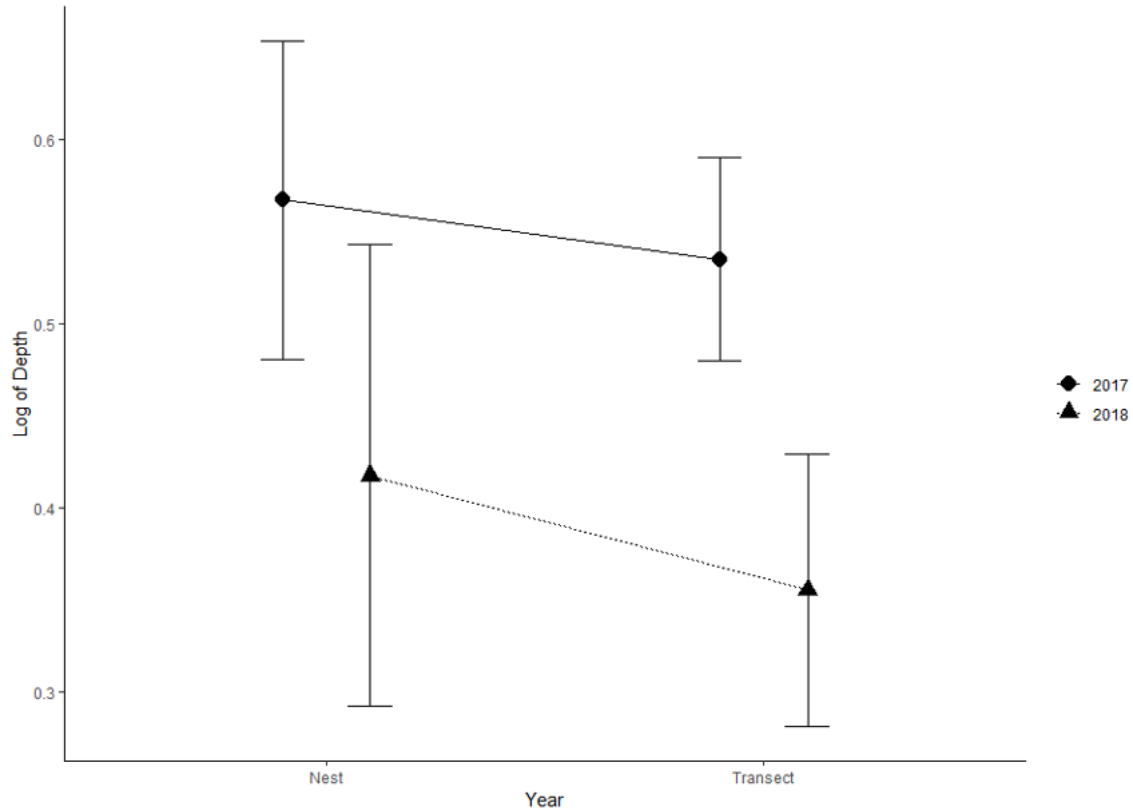


Figure 3. Interaction of used and available depths among two sampling years (2017 & 2018). Plotted values are least square means (\pm standard error) from ANOVA model.

Table 4. Linear regression model results for water depth used at Bartram’s Bass nests and available in transects in the upper Savannah River in 2017 and 2018.

Effect	$F_{1, 370}$	p
Transect	1.9	0.1722
Year	11.5	0.0008
Transect: Year	0.19	0.6635

Bartram's Bass used a variety of substrates for nesting, largely dependent upon those available in the slow velocity pockets they select for. The preferred substrate used in nests in both breeding years combined was primarily silt (36%), cobble (31%), and gravel (21%), whereas the most available substrate observed in transects was bedrock (23%) and cobble (23%). Bedrock and cobble were the most available substrates in both 2017 (bedrock, 19%; cobble, 22%) and 2018 (bedrock, 34%; cobble, 26%). However, in 2017 bass used silt (41%) and cobble (41%) habitats more than they were available (silt, 9%; cobble, 22%) ($p < 0.0001$), and in 2018 they used gravel (58%) and silt (25%) more than they were available (gravel, 8%; silt, 16%) ($p < 0.0001$) (Figure 5). On average, nests were 1.84 ± 0.25 m from the nearest bank, and 4.67 ± 0.56 m from the nearest upstream flow influence.

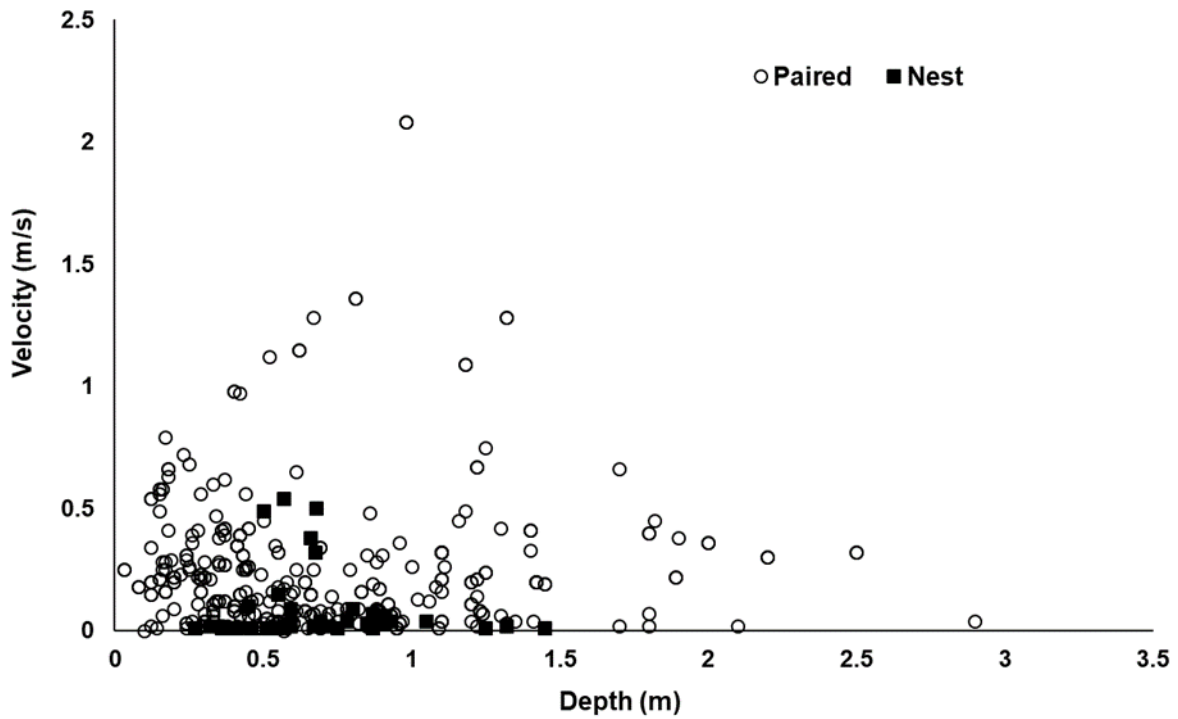


Figure 4. Velocities and depths used at nests compared to those available based on habitat transect data for 2017 and 2018 nesting seasons combined. Bartram’s Bass were observed using water depths less than 1.5 m and water velocities less than 0.54 m/s. 33 of the 39 (85%) Bartram’s Bass nests were found in areas of less than 0.1 m/s velocity.

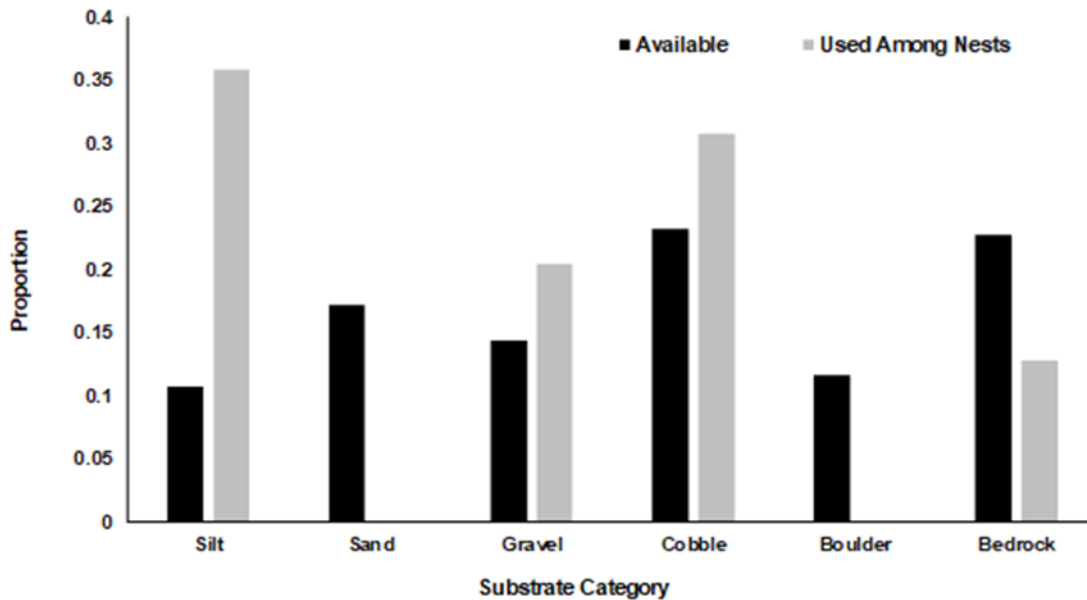


Figure 5. Substrates used at nests compared to those available based on habitat transect data for 2017 and 2018 nesting seasons combined. Though available substrate was dominated by bedrock and cobble, bass selected silt, cobble, and gravel more than they were available. Each category (“Available” versus “Used Among Nests”) represents a proportion of substrate availability, and when summed equals 1.0.

Discussion

Slow water velocities appeared to be the strongest microhabitat variable selected by nesting Bartram’s Bass in the upper Savannah River. Of the 39 pure nests found over both seasons, 33 (85%) occurred in velocities less than 0.10 m/s. Placement of nests also indicated that slow velocities may be a key requirement for nest sites. Individual nests were consistently located near the shore, and downstream of a major flow influence in pockets of slow water velocity which served as refugia from fluctuating water current. Although a few nests were found in higher velocities (0.30-0.60 m/s), these were observed just after large rain events, suggesting that it is unlikely Bartram’s Bass would

select these higher velocities at baseflow conditions. The conclusion that lower velocities will be selected for when they are available was also supported by interannual difference in water velocities measured at nest sites. During the 2018 nesting season, when numerous rain events occurred, Bartram's Bass always selected for areas of slower water velocities compared to 2017 which was a drier spring. Results of this study are similar to other studies that investigated nesting and seasonal use preferences of other riverine black basses. Strong (2010) found that Suwannee Bass in Ichetucknee River, FL nest in similar water velocities (\bar{x} = 0.01 m/s). Smallmouth Bass in riverine environments have been observed nesting in high-flow refuge pockets of less than 0.03 m/s (Lukas and Orth 1995). Earley and Sammons (2015) observed Alabama Bass using slower water velocities associated with large woody debris (LWD) year round, although this study did not specifically address nesting preference. Largemouth Bass in lotic streams have been observed nesting in pools near the bank (Jenkins and Burkhead 1994). Given that Bartram's bass appears to select for low velocity habitats, it seems logical that high velocity discharge events may negatively affect recruitment if such events reduce nesting success. While this hypothesis was not investigated in the current study, some Shoal Bass and Smallmouth Bass populations have been negatively impacted by flashy hydrology due to impacted recruitment (Lukas and Orth 1995; Taylor et al. 2018).

Although results suggest Bartram's Bass do not select for a narrow range of depth, 90% of nests were found in less than a meter of depth. Bartram's Bass nested in a wide range of depths (0.27 m to 1.45 m) that were similar to overall available depths. This is similar to the Suwannee Bass, which also nest in a wide range of depths (0.33 m

to 1.37 m) (Strong 2010). Smallmouth bass have, conversely, been observed nesting at depths higher than those observed in this study ($\bar{x}= 1.09 \pm 0.28$ m) (Lukas and Orth 1995). Alabama Bass have been observed using depths greater than 1.09 m in spring and summer, which suggests they may use greater depths for nesting (Earley and Sammons 2015).

Bartram's Bass selected for silt, gravel, and cobble in greater proportion than they were available during both nesting seasons. Bass used smaller substrates than in 2018, consistent with the slower microhabitats they selected overall. We observed bass nesting over all substrate categories, depositing eggs in both defined bowls or broadcasting them over bedrock and detritus. Thus, while the substrate selection results are statistically significant, they are not likely biologically significant. Bartram's bass likely do not actively seek out particular substrates, but instead seem to select whatever substrate is available, given the optimal current velocity and distance from bank or shelter. Earley and Sammons (2015) observed Alabama Bass using a variety of substrates throughout nesting season, however they used bedrock more than anything else in spring and summer. Smallmouth Bass have been observed preferring rocky substrates in high current velocities (Rankin 1986; Todd and Rabeni 1989), and Spotted Bass prefer fine substrate and woody debris (Scott and Angermeier 1998).

The results of this study offer insight into the reproductive life history of Bartram's Bass and how important it is to study spawning activity throughout multiple nesting seasons. By observing a nesting season with increased rainfall in 2018, we were able to see that Bartram's Bass responded by selecting pools of slower moving water in

every nesting attempt documented. Bartram's Bass exhibited advantageous strategies to natural reproduction, evidenced by the numerous spawning events that coincided with flow fluctuations, and the selection of flow refuge areas in the year of higher flow. Because annual stochastic events are typical throughout the Bartram's Bass range in the Savannah River, access to quality nesting areas is crucial to maintaining stable populations (Orth and Newcomb 2002). Due to the limited range of Bartram's Bass and potential for future habitat degradation, managers should carefully consider protecting and restoring important nesting microhabitat for this species in the Savannah River.

Bartram's Bass nest characteristics differed starkly from those observed in the Shoal Bass, which share a most recent common ancestor (Freeman et al. 2015). Bartram's Bass nest bowls ranged from 10 cm to 95 cm in diameter, whereas Shoal Bass nests were typically contained within 30 cm diameter with no obvious concave profile (Bitz et al. 2015). Shoal Bass make long migrations to spawning shoals in the spring before nesting (Sammons and Gocłowski 2012; Gocłowski et al. 2013). While movement of Bartram's Bass remains unstudied, most Bartram's Bass nests did not use shoal structures, even when available. Shoal Bass also nest in areas directly behind flow influences or upstream of a riffle, typically closer to swifter water current, and select sand-gravel substrates (Bitz et al. 2015). Conversely, Bartram's Bass nest closer to shore and prefer silt, cobble and gravel substrates. These results indicate that assuming ecological requirements from phylogenetic relationships may be problematic in this group of fishes. Understanding species-specific requirements for reproductive habitat use and other life history requirements will be critical for conserving endemic black basses.

The black bass clade is made up of both rare endemics and highly sought-after sport fish species, many of which co-occur and share similar habitats (Jackson 2002). In areas where nonnative congeners have been introduced, the use of similar habitats for reproduction poses a major potential risk of genetic introgression (Anderson 1953; Todd and Rabeni 1989; Perkin et al. 2010). Future work should identify nonnative black bass species nesting preferences in the upper Savannah River. This study can serve as a model for future research in areas where these populations persist in conjunction with nonnative species, further allowing us to assess how species' microhabitat selection may drive hybridization.

CHAPTER TWO

SPATIAL DISTRIBUTION OF BARTRAM'S BASS AND CONGENERS IN THE SAVANNAH RIVER BASIN

Introduction

Species can be transported outside their native ranges by deliberate and unintentional introduction (Pyšek and Richardson 2010), natural introduction, or may become invasive within their native ranges (Scott and Helfman 2001). Nonnative species introductions can have detrimental impacts on native organisms, although only a fraction successfully establish and become invasive (Williamson and Fitter 1996; Allendorf and Lundquist 2003; Pyšek and Richardson 2010). Invasive species pose major threats to biodiversity, ecosystem stability, agriculture, fisheries and public health (Lee 2002). Invasions cause communities to form which were originally absent in the ecosystem, resulting in novel interactions between species that would not have existed otherwise, such as competition between the nonnative and native species, declines in the native populations, and hybridization (Huxel 1999).

Hybridization is a major mechanism by which invasive species impact native species (Huxel 1999). Hybridization can occur in any system containing distinct species capable of reproducing (Rhymer and Simberloff 1996; Huxel 1999), and is common across taxa (Simberloff 1996; Schwartz et al. 2004; Latch et al. 2006). It can occur at localized scales, or broadly over a species' range depending on abiotic context and dispersal ability. Dispersal ability of fish depends on access to upstream environments, often restricted by barriers (waterfalls, dams, etc.); these barriers can sometimes be a

beacon of hope in the case of hybridization, preventing a nonnative species from accessing possible refuge habitats where natives may hold out. Extensive hybridization and subsequent introgression can result in population decline, loss of genetically distinct populations, or extinction (Rhymer and Simberloff 1996; Alvarez et al. 2015).

Hybridization can cause ‘genetic swamping’ of native genomes through introgression, often resulting in ‘hybrid swarms’ in which fertile hybrids displace native parental populations (Anderson 1953). In cases of extensive introgression, genetic differentiation between parent species can be dissolved, creating higher inheritance of maladapted genes (Huxel 1999; Alvarez et al. 2015; Bolnick 2015). Despite the dramatic effects hybridization can have on an ecosystem, the potential for and effects of interbreeding between nonnative and native individuals is an often overlooked impact produced by species invasions (Huxel 1999).

Ray-finned fishes (Actinopterygii) hybridize more frequently than other vertebrate classes, especially when co-occurring congeners use similar habitats for reproduction (Ryman and Utter 1986; Scribner et al. 2001). Hybridization is widespread among freshwater fishes, being common among many families including Esocidae, Catostomidae, Leuciscidae, Centrarchidae, Salmonidae, and Percidae (Crossman and Buss 1965; Greenfield et al. 1973; Keck and Near 2009; McKelvey et al. 2016; Eschenroeder et al. 2018). Scribner et al (2001) identified nearly 200 fish species that are threatened by hybridization. Hybridization with invasive species poses a threat to many fishes, especially those with relatively small ranges (Koppelman and Garrett 2002). Although the processes and predictors of invasion have been widely studied in fishes

(Moyle and Light 1996; Moyle and Marchetti 2006; Rahel and Olden 2008), still little is known concerning how the mechanism of hybridization impacts the native fish assemblage after an invasion in a system (Awise et al. 1997; Barwick et al. 2006; Jelks et al. 2008; Pipas, and Bulow 2011; Peterson 2015).

Black basses (*Micropterus* spp.) are an ideal group for evaluating landscape-level drivers of hybridization as many species represent small endemic populations of limited distribution, while others are heavily introduced outside their native ranges (Jackson 2002; Oswald 2007; Diedericks et al. 2018). The black basses (Centrarchidae: *Micropterus*) include some of the most widespread and popular sportfish species in the United States, and congruently the most widely introduced species (Jackson 2002; Peoples and Midway 2018). Currently, there are nine recognized species of black bass in the southern US (Near et al. 2003, Baker et al. 2013; Tringali et al. 2015), but approximately twenty may actually exist (Tringali et al. 2015). A few species in this genus have large native range sizes, but several others are restricted to single or a few river basins in the southeastern United States. Due to widespread introductions of some black bass species, many of the endemic black basses in the southeastern US are threatened by hybridization with cosmopolitan species such as Spotted Bass *M. punctulatus*, Alabama Bass *M. henshalli*, Smallmouth Bass *M. dolomieu*, and Largemouth Bass *M. salmoides* (Awise et al. 1997; Koppelman and Garrett 2002; Barwick et al. 2006; Bangs et al. 2017). For example, Guadalupe Bass, native to the Edwards' Plateau of Texas, has become extirpated in parts of its historical range due to introgression with the nonnative Smallmouth Bass (Whitmore 1983; Littrell et al. 2007),

and Shoal Bass are threatened by hybridization with Spotted Bass (Avisé et al. 1997; Alvarez et al. 2015). The transplant of some endemic species have also lead to introgression with more cosmopolitan native black bass (Pipas and Bulow 2011). Black basses are particularly prone to intrageneric hybridization due weak reproductive barriers that allow native and nonnative individuals to reproduce viable offspring (Littrell et al. 2007; Alvarez et al. 2015; Koppelman 2015; Bangs et al. 2017), and hybridization is frequently documented among this group of congeners (Whitmore 1983; Oswald et al. 2015; Dakin et al. 2015). Many studies have also investigated introgression and/or extinction by hybridization (Avisé et al 1997; Barwick et al. 2006; Littrell et al. 2007), but studies regarding the landscape-level factors that drive hybridization in fishes have largely been limited to evaluation of impacts on trout populations (Hitt et al. 2003; Boyer et al. 2008; Muhlfeld et al. 2009; Marie et al. 2012; Muhlfeld et al. 2014; McKelvey et al. 2016; Splendiani et al. 2016).

Bartram's Bass is endemic to the upper Savannah River basin of South Carolina and Georgia. Individuals have been commonly referred to throughout its range as the Redeye Bass (*M. coosae*). However, Freeman et al. (2015) identified this species to be more closely related to Shoal Bass, and supported the elevation of Bartram's Bass to species status. Bartram's Bass range extends from below the fall line of the mainstem savannah River. It has been introduced in the Saluda River of the Santee drainage (Bettinger 2015). Bartram's Bass face a multitude of threats including land-use practices, competition, and hybridization with invasive congeners, including Smallmouth Bass (*M. dolomieu*) and Alabama Bass (*M. henshalli*) (Oswald et al. 2015; Bangs et al. 2017).

Alabama Bass was introduced into the Savannah River basin in the 1980s by anglers to create a sport fishery for the species (Oswald 2007). Prior to the introduction of Alabama Bass, Bartram's Bass were found throughout reservoirs of the upper Savannah River, demonstrating the ability to tolerate reservoir habitats. Since their introduction, Alabama Bass have become widespread in the upper Savannah River basin, and are now colonizing the tributaries (Oswald et al. 2015). Bartram's Bass and Alabama Bass hybrids have been found in the tributaries; however, it is unknown to what extent hybridization is occurring. The goal of this study was to identify the distribution of Alabama Bass, Bartram's Bass, and their hybrids, in the upper Savannah River basin. We quantified effects of landscape-scale variables on the distribution of each species to aid in protecting and enhancing habitat for Bartram's Bass.

Methods

Study Area

The Savannah River basin spans 27,394 km², encompassing 15,076 km² in eastern Georgia, 11,865 km² in western South Carolina, and 453 km² in southwestern North Carolina (DHEC 2017). There are four large impoundments in the upper Savannah River basin: lakes Jocassee, Keowee, Hartwell, and Russell, as well as smaller reservoirs that impound tributaries upstream of these lakes: lakes Burton, Rabun, Tugaloo, Yonah, Secession and Stevens Creeks. Land use in the upper Savannah River basin consists of 55.3% forested land, 27.4% agricultural land, 9.3% urban land, 5.7% water cover, 1.7% forested wetland, and 0.6% barren land (DHEC 2017). The upper Savannah River is located in the Southern Blue Ridge escarpment and upper southern Piedmont ecoregions

(Omernik 1987) above the fall line. The Piedmont is heavily impacted by development and urbanization, while the Blue Ridge uplands that make up the most upstream reaches of the Savannah River are heavily forested (DHEC 2017). The inner and outer Piedmont ecoregions comprise most of the upper Savannah River watershed (Omernik 1987).

Below the fall line, the Savannah flows southeast along the border of Georgia and South Carolina before meeting the Atlantic Ocean, encompassing both the Southeastern Plains and Southern Coastal Plain regions (Omernik 1987).

We sampled 160 sites on tributaries to the upper Savannah River to quantify the factors affecting distribution of Bartram's Bass (Figure 1). Sites were selected to represent a range of stream size and gradient, elevation, watershed- and riparian-scale land use, and distance from impoundments, given access constraints. We collected bass on 300-m reaches using multiple sampling methods over two field seasons (March-November, 2017 and 2018). Upon arrival at a site, we first sampled by hook-and-line for approximately one hour, as angling is an effective sampling technique for black basses (Mycko et al. 2018). We then sampled the same reach using both single and double-backpack electrofishing depending on the size of the stream. Fin tissue was collected and preserved for genetic analysis on all captured individuals.

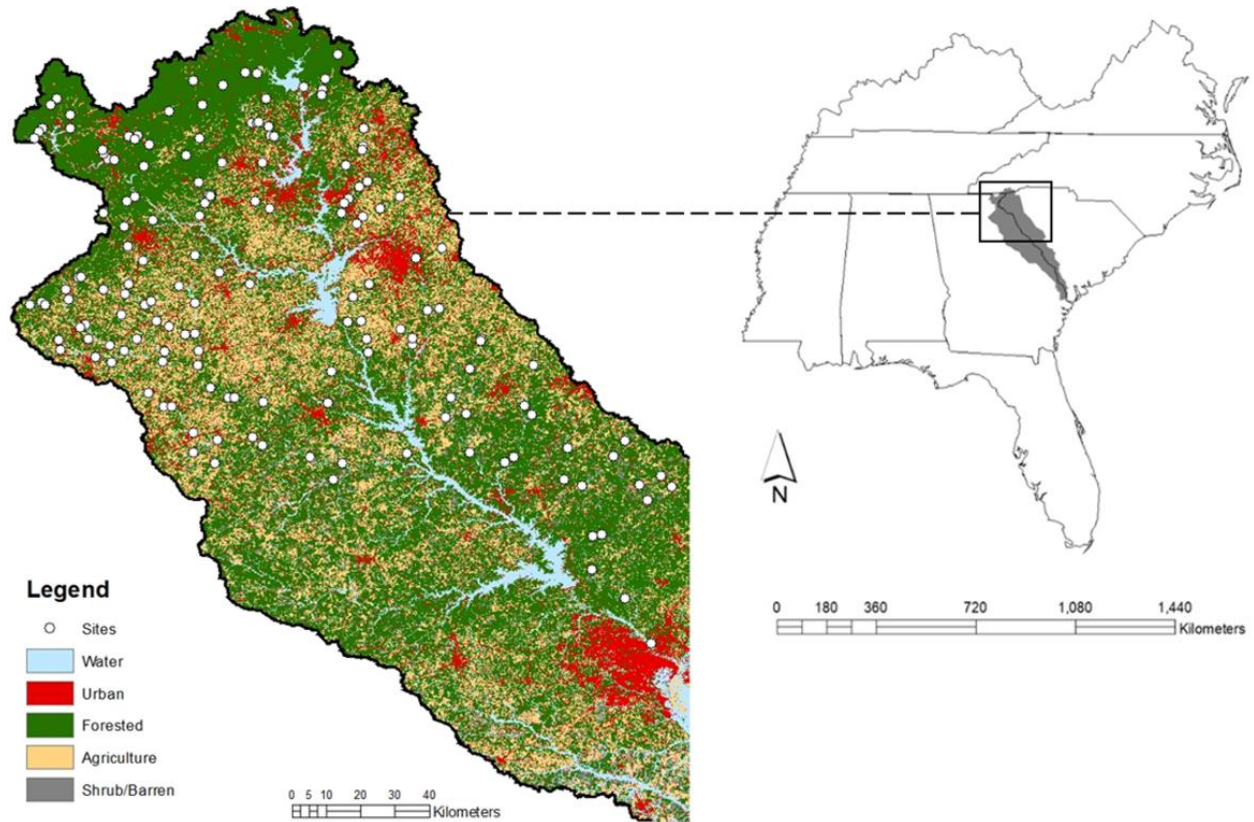


Figure 1. Map of the upper Savannah River and fish collection sites. Land use is categorized in five categories: water, urban, forested, agriculture, and shrub/barren. Management units as defined in Oswald et al. (2015) are outlined in black.

Analysis

Tissue samples of collected individuals were processed at the Hollings Marine Laboratory in the Population Genetics Laboratory of the South Carolina Department of Natural Resources (SCDNR). Markers for genetic analyses were adapted based on genetic analyses presented by Bangs et al. (2017). Individuals were classified as one of four pure species (Bartram’s Bass, Largemouth Bass, Smallmouth Bass, Alabama Bass), or as hybrid (crosses between pure species).

We gathered data from the National Hydrologic Database Plus Version 2 (NHD) and associated segment-scale attributes to compile predictor variables for a species distribution model for Bartram's Bass. Land use was reclassified from the National Land Cover Database (NLCD) 2011 into five categories: water, urban, forested, agriculture, and shrub/barren (Figure 1). Percentages of land use types at the segment scale were calculated by creating a 30-meter buffer around the stream network, and extracting 500-meter stream segments upstream of each site (Frimpong et al. 2005). Watershed-scale percent land cover was obtained through the NHD. We also included geomorphological attributes such as elevation, stream gradient, watershed area, and a binary dummy variable indicating ecoregion (Table 1). To represent distance from sources (i.e., reservoirs) of non-native congeners (e.g., Alabama Bass) as a metric to quantify dispersal potential for these non-native congeners, we calculated distance to nearest downstream impoundment as the fluvial distance from the site to the last riffle upstream of the impoundment, as identified by aerial photographs.

Table 1. List of watershed-scale predictor variables local-scale response variables used in the species distribution mode.

Variable	Description	Range of values
BTB	Whether or not Bartram's Bass were present at the site	0= No BTB; 1= BTB
Watershed Land Use	Watershed-scale percent land use classified into 5 categories	Water, Urban, Forested, Agriculture, Shrub/barren
Riparian land use	Riparian-scale percent land use classified into 5 categories	Water, Urban, Forested, Agriculture, Shrub/barren
Elevation	Elevation of stream segment	190-2,677 feet
Stream gradient	Stream gradient of stream segment	0.01-63.4 m/km
Watershed area	Area of watershed that contains a site	1.46-1,757 km ²
Ecoregion	Binary variable of whether site is in the Piedmont or Blue Ridge ecoregion	0=Blue Ridge; 1=Piedmont
Distance to reservoir (DR)	Distance from site to reservoir (last riffle)	0.21-154 km

We modeled Bartram's Bass occurrence as a binary variable by using presence/absence of pure individuals. We scaled and centered elevation, watershed area, stream gradient, and distance to reservoir variables. We then assessed the data for collinearity based on a threshold of $r=0.5$. We kept stream gradient, ecoregion, watershed area, distance to reservoir, watershed percent forested, and riparian percent forested in our model as other variables were highly correlated. As elevation was highly correlated with ecoregion, as well as forested, agriculture, and shrub/barren watershed-scale land covers. All five land cover variables were highly collinear. In our models, we retained only forested land cover from both the watershed and riparian scales, as we considered it to be the most relevant among the different land cover types. We used the *lme4* package in R version 3.4.3 (R Development Core Team, 2017) to fit a generalized linear mixed model

to quantify effects of variables, and interactions between variables and distance to reservoir. To account for repeated measures (i.e. multiple individuals) within sites, models contained a random intercept of site identity, nested within ecoregion. We tested for spatial autocorrelation of site residuals using the Global Moran's I spatial autocorrelation function in ArcGIS (ESRI 2011).

To improve interpretation of GLMM interaction terms, we used conditional inference trees (CITs) to classify sites based on presence or absence of pure Bartram's Bass. CITs classify response variables by constructing sequential binary splits (nodes) in a matrix of predictor variables defined by a certain threshold (in this case, the presence or absence of Bartram's Bass; De'ath & Fabricius, 2000). No post-hoc cross-validation procedures are necessary for CITs (Hothorn et al. 2006), as CITs nodes are based on variable significance tests unlike traditional regression trees. For this analysis, we used the same suite of variables as in the GLMM, only unstandardized. This provides more interpretable thresholds of predictor variables. We fit CITs using the *ctree* function in the *party* package and specified that nodes be split based on univariate partitioning with $p \leq 0.05$. We assessed overall model fit of CITs based on the area under the receiver-operating curve (AUC), and accepted values greater than 0.70 as an adequate model fit.

Results

A total of 787 individuals were collected at 77 sites in 2017 and 2018. Genetic results of a subsample of 241 individuals from 51 sites are included in the current analyses. This subsample was comprised of roughly 5 individuals per site available at the time of genetic analyses. Of these 51 sites, 11 are from the Blue Ridge and 40 from the

Piedmont ecoregions. Of those individuals analyzed, 110 samples were pure Bartram's Bass, 97 were Largemouth Bass, 33 were hybrids, and 1 was a pure Alabama Bass. We found exclusively pure Bartram's Bass at only 10 sites, but pure individuals were present at 32 sites, and persisted with congeners at 22 of 51 sites. Hybrids were present at 21 sites, and were rarely found exclusively. Bartram's Bass were not found at 18 of the 51 sites included in the analyses (Figure 2).

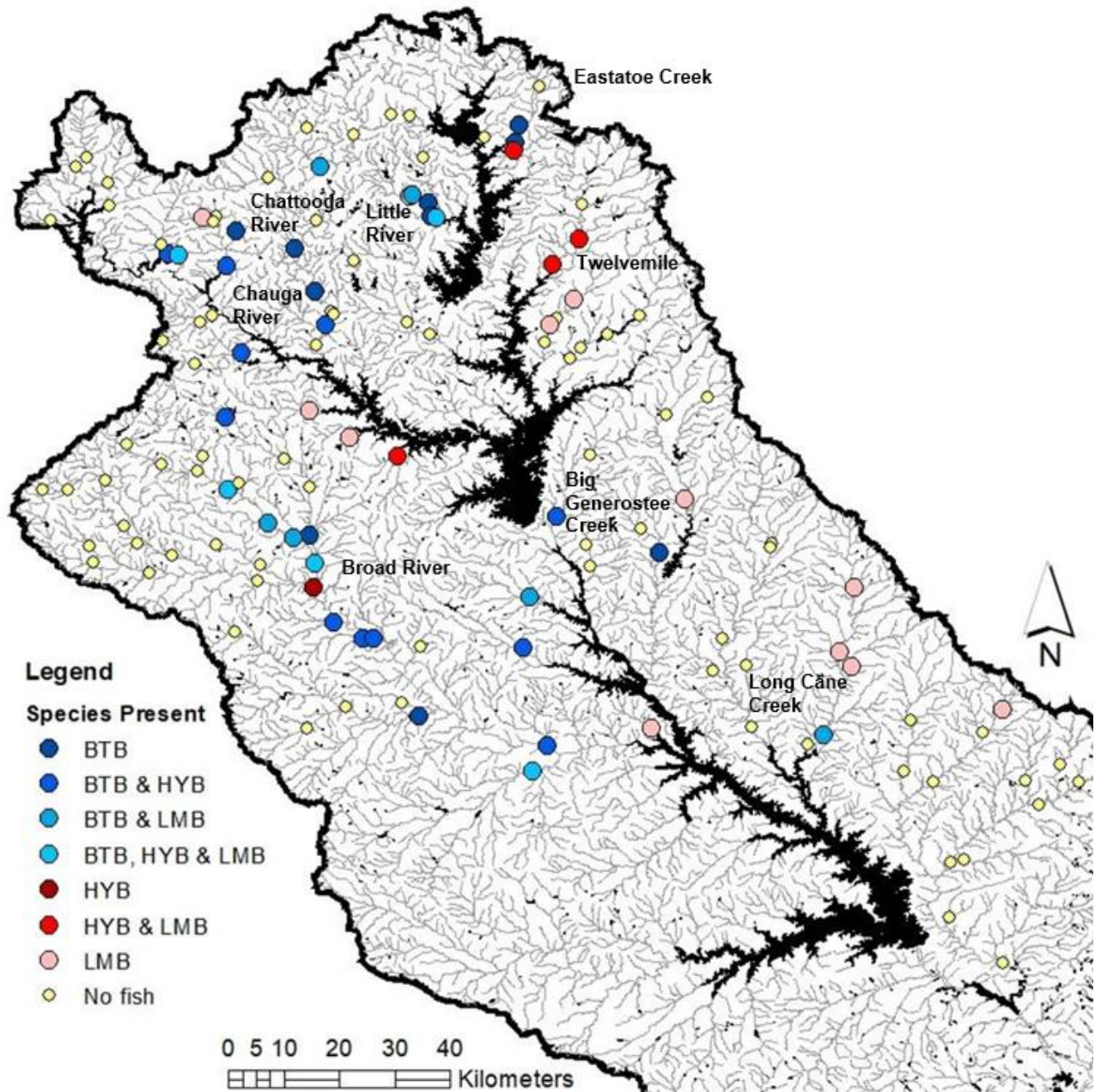


Figure 2. Map of sites in the upper Savannah River basin that are included in the analyses. Sites are color-coded with species present at each site; blue shades represent sites with Bartram’s Bass. “No fish” refers to the lack of black bass.

Generalized linear mixed models revealed forested land cover at the watershed scale was the strongest predictor of Bartram’s Bass occurrence. Stream gradient, distance to reservoir, and watershed area did not have significant effects. However, distance to reservoir interacted significantly with stream gradient and watershed-scale forested land cover to influence occurrence of Bartram’s Bass. No interaction was found between distance from reservoir and watershed area, or distance from reservoir and riparian forested land cover (Table 2). Model residuals failed the Moran’s I spatial autocorrelation test ($p= 0.2556$).

Table 2. Generalized linear mixed effects model results for Bartram’s Bass occurrence in the upper Savannah River.

Effect	Parameter estimate	Standard Error	Z	p
Distance to reservoir (DR)	0.53	0.51	1.05	0.2930
Forested riparian	0.55	0.39	1.41	0.1589
Forested watershed	1.01	0.45	2.26	0.0236
Stream gradient	0.54	0.48	1.11	0.2660
Watershed area	0.17	0.48	0.35	0.7260
DR : forested riparian	-0.15	0.42	-0.37	0.7141
DR : forested watershed	-1.42	0.61	-2.31	0.0210
DR : watershed area	0.29	0.42	0.70	0.4857
DR : stream gradient	2.10	0.75	2.81	0.0049

Conditional inference trees helped to inform GLMM results for black bass occurrence at survey sites. The CIT had an AUC value of 0.74, indicating acceptable model fit. As in the GLMM, watershed-scale forested land cover was clearly the most important classifying factor in the CIT (Figure 3); there was the greatest probability of Bartram’s Bass occurring in sites with watershed-scale forested land cover above 68% with stream gradients less than 8.5, that are greater than 2.5 km from a reservoir.

However, distance to reservoir and watershed area contributed to subsequent splits among sites of less than 68% forested watersheds. Sites with less forested cover, and larger watershed areas overall contained higher probability of hybrid presence, however forested cover at the watershed scale contributed to a subsequent split, where sites with less forested cover represented presence of Bartram's Bass, hybrids, and Largemouth Bass. Sites with less watershed area and greater distance from reservoirs are more likely to contain no bass, and those closer to reservoirs were more likely to harbor Largemouth Bass (Figure 3).

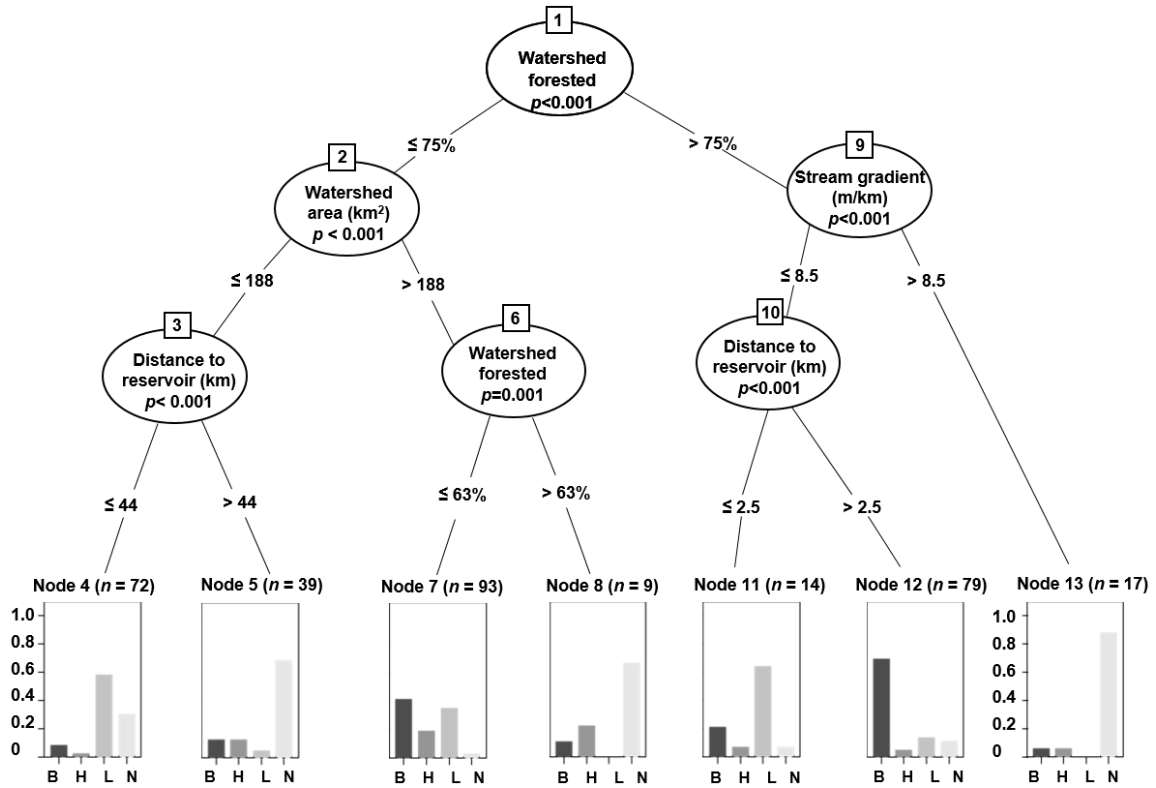


Figure 3. Conditional inference tree classifying predictors of Bartram's Bass occurrence. Splits are based on variable-wise univariate significance tests at (α)= 0.05. Bar plots represent probability of occurrence of black bass species (“B” = Bartram’s Bass, “H” = Hybrid, “L” = Largemouth Bass, “N” = None). Numbers on the right of histograms represent predicted probability of Bartram’s Bass occurrence.

Discussion

Our findings provide evidence of the widespread nature of introduction and hybridization in the introduced black basses throughout Bartram’s Bass range within the Savannah River Basin. Hybridization was observed in Twelvemile Creek, Eastatoee Creek, Little River, Chattooga River, Chauga River, and throughout the Broad River. No pure Bartram’s Bass individuals were collected in the southeastern portion of the upper basin, although Largemouth Bass dominated in this area and were widespread among our

sampling sites. Although Bartram's Bass and Largemouth Bass co-occur at many site, there has not yet been evidence of hybridization between these species. Among hybrids, there was little evidence of hybridization between Bartram's Bass and Smallmouth Bass, with just two hybrid individuals occurring at one site. This evidences that the two species are capable of hybridizing, however their ranges in the upper Savannah River tributaries prevent hybridization from occurring in many systems. Hybridization between Bartram's Bass and Alabama Bass was widespread and frequent. In streams where Bartram's Bass were present, pure populations were typically observed farther upstream in the system.

Throughout the upper Savannah River basin, it appears there are very different patterns of black bass presence among distinct management units which were outlined in Oswald et al. (2015). Pure Bartram's Bass individuals were present in the Tugaloo River, Seneca River, and Upper Savannah management units, but not in the Middle Savannah. However, Bartram's Bass were largely absent from the eastern side of the upper Savannah River basin. Bartram's Bass were found throughout the Broad, Little, Chattooga, and Chauga Rivers. Largemouth Bass dominate the southeastern portion of the upper basin. Some Jocassee and Tugaloo reservoir tributaries show presence of Bartram's Bass, despite close proximity to the reservoir.

Reservoirs may be considered a source of nonnative species, as they are hotspots for sport fish introduction (Harbicht et al. 2014). The farther from the reservoir an individual is, the more removed it is from some of the physical and biological impacts of reservoirs, such as habitat simplification, and nonnative species (Falke and Gido 2006). Distance of native individuals from the reservoirs facilitates the effects of abiotic factors,

and allows for interpretation of effects driving dispersal. Our results indicate that pure Bartram's Bass are more likely found in areas of greater forested cover with smaller stream gradients that are farther from the reservoirs; Bartram's Bass were three times more probable at distances greater than 2.5 km from the reservoir even when watershed forested land cover was ideal. Therefore, distribution of Bartram's Bass mediates the effects of stream gradient and forested cover. Similarly, Harbicht et al. (2014) found that distance to the lake was a strong predictor of admixture between wild and hatchery trout. Overall, our results indicate that Bartram's Bass individuals are currently residing in mid-stream locations, as opposed to upstream locations that are too small and possibly too cold and downstream locations harboring nonnatives and increased habitat disturbance.

Many studies have assessed spatial predictors of hybridization between trout species (Hitt et al. 2003; Boyer et al. 2008; Muhlfeld et al 2009; Wagner et al. 2013; Harbicht et al. 2014; McKelvey et al. 2016; Splendiani et al. 2016; Young et al. 2016). Studies have found that native fishes are generally more likely to be replaced by nonnatives in areas altered by land use disturbance (Bunn and Arthington 2002; Largiadèr 2008), where availability and quality of habitats diminishes and subsequently diminishes the native taxa (Muhlfeld et al. 2009). Our results suggest that forest cover at the watershed scale is the only significant factor in predicting the presence of Bartram's Bass individuals; however, distance to reservoir interacted significantly with forest cover and stream gradient, suggesting that forest cover and stream gradient are important, but only in the context of distance from the reservoir. Practically, this is because although quality habitats may exist close to reservoirs, it is less likely that Bartram's Bass

individuals will be found in these areas. The evidence that hybrid presence increases with decreasing forested cover at the watershed scale suggests that hybrids tend to do better in areas altered by land use disturbance. Furthermore, forest cover at the riparian scale was not a significant predictor of Bartram's Bass occurrence, suggesting that individuals are not as impacted by local-scale impacts.

Studies of landscape-level drivers of hybridization have found similar results to ours, in that factors influencing hybridization are often intertwined and complex; for example, McKelvey et al. (2008) found that increased disturbance (road crossings) and increased temperature resulted in increased levels of hybridization. Similarly, Young et al. (2016) found that introgression between trout species was driven by warmer water temperatures, larger-sized streams, and eastern locations. Converse to our findings, land cover at the riparian scale better predicted Shoal Bass presence than at the watershed scale in the Apalachicola-Chattahoochee-Flint (ACF) Basin (Taylor et al. 2017). This is likely due to the fact that Shoal Bass are habitat-specialists who require particular types of stream habitats for different stages of their life history (ie. reproduction: shoal habitats).

Range loss is a common result of hybridization in native black bass populations (Jackson 2002; Koppelman and Garrett 2002; Littrell et al. 2007; Dakin et al. 2015; Earley and Sammons 2015; Nagid et al. 2015; Peterson 2015). Bartram's Bass were found in reservoirs prior to, and after, the introduction of nonnative congeners (Barwick et al. 2006; Oswald 2007; Bangs et al. 2017). However, Bartram's Bass in two reservoirs of the Savannah River have recently been observed as extirpated, and numbers are in

rapid decline in two more (Barwick et al. 2006; Oswald 2007; Oswald et al. 2015; Bangs et al. 2017). There is considerable variation in affinity for lentic habitats among the black basses. In their native range, Redeye Bass inhabit small 3rd or 4th order streams with cooler temperatures, and have been found at gradients of 4-7 m/km in the Coosa drainage (Kelly et al. 1981; Koppelman and Garrett 2002). Conversely, Alabama Bass inhabit medium- to large-sized rivers and do well in impoundments of the Mobile River basin (Rider and Maceina 2015), and have maintained healthy populations in impoundments where they are introduced (Pierce and Van Den Avyle 1997; Moyle 2002; Bangs et al. 2017). In the Savannah River, all four species of black bass exhibit some tolerance for lentic systems. Bartram's Bass have demonstrated the potential to thrive in areas of lower stream gradients when unaltered by nonnative congeners (Leitner et al. 2015). Our results show that Bartram's Bass populations are now found less in areas closer to reservoirs with lower stream gradients overall regardless of habitat quality, and instead persist farther upstream in tributaries. Because Bartram's Bass were found in healthy numbers in the reservoirs of the upper Savannah River prior to Alabama bass introduction, there is reason to believe their populations close to the reservoirs would follow a similar trend of decline as Alabama Bass dispersed from reservoirs into low gradient stream habitats. Trends similar to those of this study have been concluded in other *Micropterus* species facing similar threats; Shoal Bass in the ACF basin are restricted to relatively small areas of its native range due to the influence of nonnative congeners, land cover, and fragmentation (Taylor et al. 2017). It is speculated that interactions with congeners has caused exclusion of Redeye Bass from reservoirs (Parsons 1954; Barwick and Moore

1983; Koppelman and Garrett 2002). Guadalupe Bass have also experienced hybridization with Smallmouth Bass throughout their range and, prior to recent reintroduction efforts, their pure populations were nearly extirpated (Koppelman and Garrett 2002).

Many tributaries to the Savannah River impoundments contain structures once thought to be potential barriers to upstream fish movement, which may guard the pure populations that occur above barriers; generally, pure individuals of Bartram's Bass have previously been observed persisting above barrier structures (natural and anthropogenic) in many systems (Coneross Creek, Chauga River, and Stevens Creek), and intermingling with hybrids above barriers in other systems (Twelvemile River and Little River). Our results indicate that there are hybrid individuals found above some barriers (Tallulah River, Chattooga River, Twelvemile Creek, and Little River). It is likely the hybrid individuals found above barriers is a symptom of anthropogenic introduction above barriers. Management practices best suited for retaining pure pockets of Bartram's Bass may include keeping a barrier to prevent invasive movement further upstream, and subsequently educating the public about impacts of nonnative species and limiting the translocation of species outside of their native range (Bean et al. 2013).

Estimating abiotic-based predictive distributions aids in our ability to quantify species habitat relationships, range-loss estimation, remnant distributions, and allows for identification of suitable restoration sites if necessary for future management (Guisan and Thuiller 2005). The purpose of this study was to identify the abiotic factors that contribute to the dispersal of riverine black bass in the Savannah River. Developing

conservation strategies for species is particularly difficult without information specific to populations, therefore evaluating factors affecting individuals is important to the conservation of species (Rabeni and Sowa 1996). Understanding how abiotic factors influence fishes is an established concept (Wiens 2002; Gozlan et al. 2010), and is necessary for effective management of rare endemic species. Future research on rare black bass populations should implement landscape-level analyses, like those presented here, to further understand drivers of distribution within native ranges.

There are a variety of management measures that could be taken to conserve pure pockets of Bartram's Bass. Management should seek to restore habitat at the watershed scale for hybrid-influenced areas, and focus on maintaining habitat for pure individuals. Riparian-scale forested cover had little effect on Bartram's Bass distribution, therefore restoration at the local riparian scale would not likely have much of an impact on the population. Conservation stocking may be an option for this species to reverse genetic effects of introgression in some stream segments. Such stocking has been implemented successfully in pockets of Guadalupe Bass in the South Llano River of Texas (Bean et al. 2013) and in pockets of Shoal Bass in the Chattahoochee River, below the Morgan Falls Dam of Georgia (Taylor et al. 2018). Although stocking would not ensure conservation of a pure population, stocking has the potential to overwhelm the gene pool with native alleles. For this method to be successful for Bartram's Bass, stocking efforts would have to focus on areas of suitable habitat, and/or in locations where hybrids have not already dominated. Suitable sites may include those in watersheds of greater than 75% forested cover, at least 2.5 km from a reservoir, with stream gradient under 8.5; suitable habitat

should also consider areas for reproduction consisting of slow water velocity (<0.1 m/s) pockets along stream banks. Stocked individuals would need to be reared from brood-stock that has been screened against nonnative alleles to ensure pure genetics are being contributed to the natural population, and should consider management units based on genetic provinces identified by Oswald et al. (2015). Restoration stocking efforts have been successful for the Guadalupe Bass, reducing hybridization rates with smallmouth bass by up to 9% per year (Fleming et al. 2015). However, this method is costly, and would require heavy public involvement to be successful. Another option would be the removal of nonnative individuals where they occur, however this method requires a tactical approach to avoid missing hybrids and nonnative species in systems where they could continue to spread. This approach may be insufficient on its own, as it is unlikely managers would be able to remove enough individuals to prevent future reproduction; furthermore, field identification of hybrid individuals can be difficult. Possibly a combination of methods may be best for prolonging pure populations of Bartram's Bass. Furthermore, due to the relative lack of public knowledge surrounding this species within its native range, management actions should seek to educate and advocate for Bartram's Bass whenever possible. Future directions should seek to find proper and realistic management solutions for this species.

GENERAL CONCLUSION

Bartram's Bass is an endemic black bass found only in the Savannah River basin of South Carolina and Georgia. This research was initiated after previous South Carolina Department of Natural Resources (SCDNR) sampling of tributaries revealed that Bartram's Bass and their hybrids with nonnative congeners, primarily Alabama bass, were co-distributed in some tributaries. Thus, we set out to define the nesting preferences of Bartram's Bass, and to determine the distribution of current pure Bartram's Bass individuals and the factors driving them.

Results of this study shed light on how we may better manage pure populations moving forward. Over the two spawning seasons, we detected 75 nests, of which 39 were genetically identified as pure Bartram's Bass. We found that water velocity was the most important factor for nesting Bartram's Bass. Specifically, we observed that individuals select slow-moving pockets near shore for nesting, and particularly for refuge during years of increased flow. We conclude that depth did not play a role in nest selection, as nesting individuals selected for a variety of depths. Bartram's Bass used a variety of substrates for nesting, largely dependent upon those available in the slow velocity pockets they select for. The preferred substrate used in nests in both breeding years combined was primarily silt (36%), cobble (31%), and gravel (21%), whereas the most available substrate observed in transects was bedrock (23%) and cobble (23%). On average, nests were 1.84 ± 0.25 m from the nearest bank, and 4.67 ± 0.56 m from the nearest upstream flow influence. Our results provide knowledge of quality nesting

habitats for endemic Bartram's Bass, which will be critical for future management of this species and our understanding of hybridization with nonnative congeners.

This study documents where different black bass species are found in the tributary systems, and the factors that have a role in their distributions. Pure Bartram's Bass were observed in the Broad, Little, Chattooga, and Chauga Rivers, as well as sites in close proximity to Lake Jocassee. Hybrids were mainly observed in tributaries of the northeastern portion of the upper Savannah River basin, but also co-occurred with pure Bartram's Bass individuals. There was a lack of Bartram's Bass individuals in the southeastern portion of the upper basin. Largemouth Bass were also widespread among our sampling sites. Among hybrids, there was little evidence of hybridization between Bartram's Bass and Smallmouth Bass, and high evidence of Bartram's Bass and Alabama Bass hybridization. No hybrids were identified as Bartram's Bass and Largemouth Bass, similar to results of previous SCDNR sampling. In streams where Bartram's Bass were present, pure individuals were typically observed farther upstream in the system.

Results of this study suggest abiotic factors play a role in determining occurrence of pure Bartram's Bass, and that future land management activities could have an impact on this species. Our results indicated that forested land cover at the watershed scale was the only significant predictor of Bartram's Bass occurrence. Stream gradient, watershed area, and distance to reservoir were also found as key mechanisms in determining Bartram's Bass presence. As such, fewer Bartram's Bass individuals were found closer to reservoirs even when forested cover and stream gradient was at ideal levels. This

suggests that stream gradient and forested cover are important, however only in the context of distribution from reservoirs.

Based on the results of this study, management of Bartram's Bass should focus on areas of the basin that still harbor pure individuals, and those that have the potential to host successful pure populations. Land management of the northwestern region is dominated by federal and state managed lands that are mostly protected from future development and pollutants; these areas may therefore be the most promising when considering future management. The Broad River also harbors many sites with pure individuals, as well as sites where hybrids and pure coexist; this may be a system to consider for future management. Efforts to combat the spread of hybridization have been successful in other systems when stocking of the native species, and eradication of nonnative and hybrid individuals are implemented together (Bean et al. 2013; Fleming et al. 2015). It would be wise to select locations for this type of management that incorporate appropriate habitats for Bartram's Bass, as defined in this study; suitable sites may include those in watersheds of greater than 75% forested cover, at least 2.5 km from a reservoir, with smaller stream gradients; suitable habitat should also consider areas for reproduction consisting of slow water velocity (<0.1 m/s) pockets along stream banks. Managing for pure Bartram's Bass should be of utmost importance moving forward, as we have observed a lack of Bartram's Bass individuals in areas that they were previously found, specifically in the eastern portion of the upper basin. Trends of hybridization in other endemic populations of black bass have provided cause to act quickly to prevent further spread of nonnative species in this basin. It is important to consider how various

management actions have fared in other populations of rare black basses experiencing similar threats in their respective ranges. Next steps for management of Bartram's Bass should implement the results of this study in decision-making.

Hybridization is a mechanism that acts quickly on native populations (Huxel 1999). Since their introduction into the Savannah River Basin, Alabama Bass have dominated the reservoir systems, and spread into tributaries. We found that hybrids of these nonnative species and Bartram's Bass occur in mid-upstream locations, with the exception of few pure populations protected by barriers. Although hybridization between Bartram's Bass and Smallmouth Bass was documented at a small amount, it should be monitored and taken into consideration for future management. Future studies and management should investigate the reality and implications of implementing eradication for nonnative species and/or stocking efforts for Bartram's Bass throughout their range in the upper Savannah River basin.

Appendix A

Supplemental Tables

Table A.1. Sites included in chapter one analyses. Table include site identities, coordinates, and number of nests found at each site as well as the number of pure Bartram's Bass nests found at each site.

Site	Latitude	Longitude	Nests	Pure
SC01	34.9719	-83.1147	0	0
SC02	34.9193	-83.1686	31	12
SC03	34.8155	-83.3065	14	10
SC04	34.7547	-83.3267	4	2
SC05	34.8327	-83.1748	0	0
SC06	34.7873	-83.2104	7	4
SC07	34.7179	-83.1772	0	0
SC08	34.6856	-83.1514	0	0
SC09	34.6636	-83.1603	0	0
SC11	34.6675	-83.0283	0	0
SC12	34.6497	-82.9916	0	0
SC13	34.7690	-83.0114	1	1
SC14	34.8717	-83.0376	0	0
SC15	34.8724	-83.0239	0	0
SC16	34.8741	-83.0203	0	0
SC17	34.8621	-82.9928	2	0
SC18	34.8405	-82.9893	0	0
SC19	34.8367	-82.9799	3	0
SC20	34.9867	-82.8458	7	5
SC21	34.9585	-82.8526	1	1
SC22	34.9464	-82.8555	0	0
SC36	34.6823	-83.1451	1	1
SC37	34.6819	-83.1468	3	3
SC38	34.8713	-83.0088	0	0
SC39	34.8442	-83.0170	0	0
GA06	34.7573	-83.3966	0	0
GA08	34.6676	-83.3649	1	0
Total			75	39

Table A.2. Sites of fish collection for Chapter 2. Included are site identifiers and coordinates.

Site	Latitude	Longitude	Site	Latitude	Longitude
DNR 000	34.3337	-82.6480	DNR31	34.3834	-82.5772
DNR 04	34.2956	-82.6192	DNR64	34.3534	-82.7861
DNR 109	34.2742	-82.7322	DNR66	34.2401	-82.3018
DNR 111	34.3098	-82.4370	GA01	34.9019	-83.2538
DNR 1111	34.3102	-82.6186	GA02	34.8394	-83.3370
DNR 1112	33.5147	-81.9935	GA03	34.8382	-83.3598
DNR 1113	34.2306	-82.4678	GA04	34.7789	-83.4154
DNR 1114	33.9529	-81.9681	GA05/06	34.7770	-83.3985
DNR 1115	33.9241	-81.9387	GA07	34.6788	-83.3441
DNR 117	33.6314	-82.0614	GA08	34.6676	-83.3649
DNR 145	34.0133	-82.4682	GA09	34.6193	-83.2977
DNR 157	33.9277	-82.0248	GA10	34.5262	-83.1854
DNR 168	34.3050	-82.4391	GA11	34.4821	-83.1223
DNR 2	34.1132	-82.4776	GA12	34.4512	-83.0423
DNR 222	34.3086	-82.7373	GA13	34.5136	-83.3221
DNR 23	33.7947	-82.1462	GA14	34.4020	-83.1870
DNR 333	34.3555	-82.7517	GA15	34.3231	-83.1864
DNR 444	34.4197	-82.7724	GA16	34.2790	-83.1776
DNR 50	34.3894	-82.5472	GA17	34.2399	-83.1790
DNR 55	34.5471	-82.5404	GA18	34.3972	-83.3186
DNR 555	33.7067	-82.1475	GA19	34.3424	-83.2541
DNR 59	34.5193	-82.6082	GA20	34.3197	-83.2130
DNR 7	34.0246	-82.2114	GA21	34.1820	-83.1470
DNR 70	34.0043	-82.0932	GA22	34.1564	-83.1004
DNR 77	33.8893	-82.0020	GA23	34.1572	-83.0832
DNR 777	33.9860	-82.3772	GA24	34.0319	-83.0093
DNR 78	34.4532	-82.7314	GA25	34.0003	-82.8857
DNR 8	33.9433	-82.2210	GA26	33.9416	-82.8252
DNR 84	33.9253	-82.1751	GA27	33.9841	-82.8012
DNR 888	34.1561	-82.5171	GA28	34.0115	-82.6325
DNR 97	33.7995	-82.1236	GA29	34.1420	-82.8394
DNR 999	34.1056	-82.5309	GA30	34.2252	-82.8284
DNR03	34.0431	-82.0613	GA31	34.9351	-83.5480
DNR100	34.1123	-82.3066	GA32	34.7936	-83.4269
DNR103	34.1352	-82.3256	GA33	34.5554	-83.2877
DNR26	34.0005	-82.3520	GA34	34.2756	-83.2670

Site	Latitude	Longitude
GA35	34.2774	-83.3727
GA36	34.3075	-83.5433
GA37	34.8582	-83.5847
GA38	34.9193	-83.5649
GA39	34.2476	-83.4038
GA40	34.8480	-83.5961
GA41	34.5517	-83.3628
GA42	34.1322	-83.2684
GA43	34.1318	-83.2486
GA44	34.0655	-83.1919
GA45	34.0125	-83.1915
GA46	34.0533	-83.0369
GA47	34.4081	-83.3017
GA48	34.4692	-83.4917
GA49	34.8331	-83.6067
GA50	34.8027	-83.4285
GA51	34.4128	-83.5186
GA52	34.4041	-83.5888
GA53	34.4386	-83.5243
GA54	34.4703	-83.4843
GA55	34.3456	-83.4730
GA56	34.4391	-83.4270
GA57	34.4269	-83.3690
GA58	34.3728	-83.3782
GA59	34.2917	-83.4088
GA60	34.2491	-83.2709
GA61	34.0461	-83.1273
GA62	33.9852	-83.1343
GA63	34.3971	-83.6191
GA64	34.1682	-83.3081
GA65	34.6380	-83.4257
GA66	34.9826	-83.1913
GA67	34.6017	-83.3727
GA68	34.4482	-83.2278
GA69	34.3080	-83.3382
GA70	34.4519	-83.3599
GA71	34.3382	-83.4877
GA72	34.2801	-83.5381

Site	Latitude	Longitude
GA73	34.3983	-83.5790
GA74	34.2630	-83.4467
GA75	34.3098	-83.4650
GA76	34.8302	-83.3427
GA77	34.8581	-83.5124
GA78	34.8940	-83.5131
GA79	34.1442	-83.0073
SC01	34.9719	-83.1147
SC02	34.9193	-83.1686
SC03	34.8155	-83.3065
SC04	34.7590	-83.3201
SC05	34.8327	-83.1748
SC06	34.7873	-83.2104
SC07	34.7179	-83.1772
SC08	34.6856	-83.1514
SC09	34.6636	-83.1603
SC10	34.6316	-83.1747
SC11	34.6675	-83.0283
SC12	34.6497	-82.9916
SC13	34.7690	-83.0114
SC14	34.8717	-83.0376
SC15	34.8724	-83.0239
SC16	34.8741	-83.0203
SC17	34.8621	-82.9928
SC18	34.8405	-82.9893
SC19	34.8367	-82.9799
SC20	34.9867	-82.8458
SC21	34.9585	-82.8526
SC22	34.9464	-82.8555
SC23	34.8125	-82.7468
SC24	34.8027	-82.7495
SC25	34.8590	-82.7450
SC26	34.7625	-82.7920
SC27	34.7190	-82.7358
SC28	34.7048	-82.7568
SC29	34.6753	-82.7845
SC30	34.6643	-82.7961
SC31	34.6364	-82.8043

Site	Latitude	Longitude
SC32	34.6796	-82.6506
SC33	34.6499	-82.7031
SC34	34.6277	-82.7469
SC35	34.6095	-82.7628
SC36	34.6823	-83.1451
SC37	34.6819	-83.1468
SC38	34.7691	-83.1158
SC39	34.9671	-82.9020
SC40	35.0041	-83.0545
SC41	35.0509	-82.8129
SC42	34.9357	-83.0018
SC43	35.0027	-83.0249

REFERENCES

- Allendorf, F.W., and L.L. Lundquist. 2003. Introduction: population biology, evolution, and control of invasive species. *Conservation Biology* 17: 24–30.
- Alvarez, A. C., D. Peterson, A. T. Taylor, M. D. Tringali, and B. L. Barthel. 2015. Distribution and amount of hybridization between Shoal Bass and the invasive Spotted Bass in the lower Flint River, Georgia. Pages 503–521 in M. D. Tringali, J. M. Long, T. W. Birdsong, and M. S. Allen, editors. *Black bass diversity: multidisciplinary science for conservation*. American Fisheries Society, Symposium 82, Bethesda, Maryland.
- Anderson, E. 1953. Introgressive hybridization. *Biological Reviews* 28: 280–307.
- Avise, J. C., P. C. Pierce, Van Den Avyle, M. J. M. H. Smith, W. S. Nelson, and M. A. Asmussen. 1997. Cytonuclear introgressive swamping and species turnover of bass after an introduction. *Journal of Heredity* 88: 14–20.
- Baker, W. H., R. E. Blanton, and C. E. Johnston. 2013. Diversity within the Redeye Bass, *Micropterus coosae* (Perciformes: Centrarchidae) with descriptions of four new species. *Zootaxa* 3635: 379–401.
- Balon, E.K. 1975. Reproductive Guilds of Fishes: A Proposal and Definition. *Journal of the Fisheries Research Board of Canada* 32: 821-864.
- Bangs, M. 2011. Decline of the Savannah River Redeye Bass (*Micropterus coosae*) due to introgressive hybridization with invasive Alabama Spotted Bass (*Micropterus punctulatus henshalli*). Theses and Dissertations.
- Bangs, M., K. J. Oswald, T.W. Greig, J.K. Leitner, D.M. Rankin, J.M. Quattro. 2017.

- Introgressive hybridization and species turnover in reservoirs: a case study involving endemic and invasive basses (Centrarchidae: *Micropterus*) in southeastern North America. *Conservation Genetics* 19(1): 57-69.
- Barwick, D. H., and P.R. Moore. 1983. Abundance and Growth of Redeye Bass in Two South Carolina Reservoirs. *Transactions of the American Fisheries Society* 112: 216–219.
- Barwick, D. H., K. J. Oswald, J. M. Quattro, and R. D. Barwick. 2006. Redeye Bass (*Micropterus coosae*) and Alabama Spotted Bass (*M. punctulatus henshalli*) hybridization in Keowee reservoir. *Southeastern Naturalist* 5: 661–68.
- Bean, P. T., D.J. Lutz-Carrillo, T.H. Bonner. 2013. Rangewide survey of the introgressive status of Guadalupe Bass: implications for conservation and management. *Transactions of the American Fisheries Society*, 142(3): 681-689.
- Berkman, H. E., & Rabeni, C. F. 1987. Effect of siltation on stream fish communities. *Environmental Biology of Fishes*, 18 (4): 285-294.
- Bettinger, J. 2015 'Bartram's' Redeye Bass.
- Bitz, R. D., P. A. Strickland, T. J. Alfermann, C. R. Middaugh, and J. A. Bock. 2015. Shoal Bass nesting and associated habitat in the Chipola River, Florida. *American Fisheries Society*, Bethesda, Maryland. 82: 237-248.
- Blackburn, T. M., Pyšek, P., Bacher, S., Carlton, J. T., Duncan, R. P., Jarošík, V., ... & Richardson, D. M. 2011. A proposed unified framework for biological invasions. *Trends in ecology & evolution*. 26(7): 333-339.

- Bolnick, D.I., K.C. Shim, and C.D. Brock. 2015. Female stickleback prefer shallow males: 522 Sexual selection on nest microhabitat. *Evolution*, 69: 1643-1653.
- Boyer, M. C., C.C. Muhlfeld, F.W. Allendorf. 2008. Rainbow trout (*Oncorhynchus mykiss*) invasion and the spread of hybridization with native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*). *Can. J. Fish. Aquat. Sci.* 65: 658–669.
- Bunn, S. E. and A.H. Arthington. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* 30: 492–507.
- Catford, J.A., R. Jansson, C. Nilsson. 2009. Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions*. 15 (1): 22–40.
- Crossman, E. J., K. Buss. 1965. Hybridization in the family Esocidae. *Journal of the Fisheries Board of Canada*, 22(5): 1261-1292.
- Dakin, E.E., B. A. Porter, B. J. Freeman, and J.M. Long. 2015. Hybridization threatens Shoal Bass populations in the upper Chattahoochee River Basin. Chapter 37: 491–502.
- Dauwalter, D. C., and W. L. Fisher. 2007. Spawning chronology, nest site selection, and nest success of smallmouth bass during benign streamflow conditions. *American Midland Naturalist* 158:60–78.
- De'ath, G., and K.E. Fabricius. (2000). Classification and regression trees: A powerful yet simple technique for ecological data analysis. *Ecology*, 81: 3178–3192.
- Diedericks, G., R. Henriques, S. von der Heyden, O.L. Weyl, C. Hui. 2018. Sleeping with

- the enemy: introgressive hybridization in two invasive centrarchids. *Journal of fish biology*, 93(2): 405-410.
- SCDHEC, S. C. Dept of Health and Environmental. 2017. DHEC: Upper Savannah River.
- Earley, L. A., and S.M. Sammons. (2015). Alabama bass and redeye bass movement and habitat use in a reach of the Tallapoosa River, Alabama, exposed to an altered flow regime. In M. D. Tringali, J. M. Long, T. W. Birdsong, & M. S. Allen (Eds.), *Black bass diversity: Multidisciplinary science for conservation* (pp. 263–280). Bethesda, Maryland: American Fisheries Society.
- Enriquez, E.J., F.P. Gelwick, J.M. Packard. 2016. Reproductive Seasonality, Courtship and Nesting in Guadalupe Bass (*Micropterus treculii*). *The American Midland Naturalist*.
- Eschenroeder, J. C., and J.H. Roberts. 2018. What Role Has Hybridization Played in the Replacement of Native Roanoke Bass with Invasive Rock Bass?. *Transactions of the American Fisheries Society*, 147(3): 497-513.
- ESRI. 2011. ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute.
- Falke J.A., K.B. Gido. 2006. Effects of reservoir connectivity on stream fish assemblages in the Great Plains. *Canadian Journal of Fisheries and Aquatic Sciences*. 63: 480–493.
- Fausch, K.D., C.E. Torgersen, C.V. Baxter, H.W. Li. 2002. Landscapes to Riverscapes:

- Bridging the Gap between Research and Conservation of Stream Fishes.
BioScience. 52:483-498.
- Fleming, B. J., G. P. Garrett, and N. G. Smith. 2015. Reducing hybridization and introgression in wild populations of Guadalupe Bass through supplemental stocking. Pages 537–547 in M. D. Tringali, J. M. Long, T. W. Birdsong, and M. S. Allen, editors. *Black bass diversity: multidisciplinary science for conservation*. American Fisheries Society, Symposium 82, Bethesda, Maryland.
- Freeman, B. J., A. Taylor, K. J. Oswald, M. C. Freeman, J. Quattro, and J. K. Leitner. 2015. Shoal basses: a clade of cryptic identity. *American Fisheries Society*, Bethesda, Maryland. 82: 449-466.
- Frimpong, E. A., Sutton, T. M., Lim, K. J., Hrodey, P. J., Engel, B. A., Simon, T. P., ... & Le Master, D. C. 2005. Determination of optimal riparian forest buffer dimensions for stream biota landscape association models using multimetric and multivariate responses. *Canadian Journal of Fisheries and Aquatic Sciences*, 62(1): 1-6.
- Goclowski, M. R., A. J. Kaeser, and S. M. Sammons. 2013. Movement and habitat differentiation among adult Shoal Bass, Largemouth Bass, and Spotted Bass in the upper Flint River, Georgia. *North American Journal of Fisheries Management* 33:56–70.
- Gozlan, R. E., J.R. Britton, I. Cowx, G.H. Copp. 2010. Current knowledge on non-native freshwater fish introductions. *Journal of fish biology*, 76(4): 751-786.

Greenfield, D. W., F. Abdel-Hameed, G. D. Deckert, and R. R. Flinn. 1973.

Hybridization

between *Chrosomus erythrogaster* and *Notropis cornutus* (Pisces: Cyprinidae).

Copeia, 1973: 54–60.

Guisan A, W. Thuiller. 2005. Predicting species distribution: offering more than simple

habitat models. *Ecology Letters* 8:993–1009.

Harbicht, A. B., M. Alshamli, C.C. Wilson, D.J. Fraser. 2014. Anthropogenic and

habitat correlates of hybridization between hatchery and wild brook trout.

Canadian journal of fisheries and aquatic sciences, 71(5): 688-697.

Hitt, N. P., C.A. Frissell, C.C. Muhlfeld, F.W. Allendorf. 2003. Spread of hybridization

between native westslope cutthroat trout, *Oncorhynchus clarki lewisi*, and

nonnative rainbow trout, *Oncorhynchus mykiss*. *Can. J. Fish. Aquat. Sci.* 60:

1440–1451.

Hothorn, T., K. Hornik, and A. Zeileis. (2006). Unbiased recursive partitioning: A

conditional inference framework. *Journal of Computational and Graphical*

Statistics, 15, 651–674.

Hubbs, Carl L. 1955. Hybridization between Fish Species in Nature. *Systematic Zoology*

4: 1–20.

Huxel, G.R. 1999. Rapid displacement of native species by invasive species: effects of

hybridization. *Biological Conservation*. 89:143-152.

Jackson, D. A. 2002. Ecological effects of *Micropterus* introductions: the dark side of

black bass. In *American Fisheries Society Symposium* 31: 221-232.

- Jelks, H. L., Walsh, S. J., Burkhead, N. M., Contreras-Balderas, S., Diaz-Pardo, E., Hendrickson, D. A., ... & Platania, S. P. 2008. Conservation status of imperiled North American freshwater and diadromous fishes. *Fisheries*, 33(8): 372-407.
- Jenkins, R. E., and N. M. Burkhead. 1993. *Freshwater fishes of Virginia*. American Fisheries Society, Bethesda, Maryland.
- Johnston, C. E. 1999. The relationship of spawning mode to conservation of North American minnows (Cyprinidae). *Environmental Biology of Fishes*, 55(1-2): 21-30.
- Johnston, C.E., and R.A. Kennon. 2007. Habitat Use of the Shoal Bass, *Micropterus cataractae*, in an Alabama Stream. *Journal of Freshwater Ecology*. 22 (3): 493-498.
- Keck, B. P., and T. J. Near. 2009. Patterns of natural hybridization in darters (Percidae: Etheostomatinae).” *Copeia* 2009 (4): 758–73.
- Kelly, H.D., E.D. Catchings, and V.W.E. Payne, Jr. 1981. Fish populations and water quality of an upland stream having two impoundments with coolwater releases. Pages 168-181 in L.A. Krumholz, editor, *Warmwater streams symposium*. American Fisheries Society, Southern Division, Bethesda Maryland.
- Koppelman, J.B., and G. Garrett. 2002. Distribution, biology, and conservation of the rare black bass species.
- Koppelman, J.B. 2015. Black bass hybrids: a natural phenomenon in an unnatural world.

- Pages 467–479 in M.D. Tringali, J.M. Long, T.W. Birdsong, and M. S. Allen, editors. Black bass diversity: multidisciplinary science for conservation. American Fisheries Society Symposium 82, Bethesda, Maryland.
- Largiadèr, C. R. 2008. Hybridization and introgression between native and alien species. In Biological invasions (pp. 275-292). Springer, Berlin, Heidelberg.
- Latch, E.K., L.A. Harveson, J. S. King, M. D. Hobson, and O. E. Rhodes. 2006. Assessing hybridization in wildlife populations using molecular markers: A case study in Wild Turkeys. *Journal of Wildlife Management* 70 (2):485–492.
- Lee, C.E. 2002. Evolutionary genetics of invasive species. *Trends in Ecology and Evolution*. 17: 386-391.
- Leitner, J.K. and L.A. Earley. 2015. Redeye Bass *Micropterus coosae* Hubbs & Bailey 1940. Pages 61–66 in M. D. Tringali, J. M. Long, T. W. Birdsong, and M. S. Allen editors. Black bass diversity: multidisciplinary science for conservation. American Fisheries Society, Symposium 82, Bethesda, Maryland.
- Leitner, J. K., K. J. Oswald, M. Bangs, D. Rankin, and J. M. Quattro. 2015. Hybridization between native Bartram’s Bass and two introduced species in Savannah drainage streams. Pages 481–490 in M. D. Tringali, J. M. Long, T. W. Birdsong, and M. S. Allen, editors. Black bass diversity: multidisciplinary science for conservation. American Fisheries Society, Symposium 82, Bethesda, Maryland.
- Littrell, B. M., D. J. Lutz-Carrillo, T. H. Bonner, and L.T. Fries. 2007. Status of an

- introgressed Guadalupe Bass population in a central Texas stream. *North American Journal of Fisheries Management* 27 (3): 785–791.
- Lukas, J. A., and D. J. Orth. 1995. Factors affecting nesting success of smallmouth bass in a regulated Virginia stream. *Transactions of the American Fisheries Society* 124:726–735.
- Marie, A. D., L. Bernatchez, D. Garant. 2012. Environmental factors correlate with hybridization in stocked brook charr (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences*, 69(5): 884-893.
- McKelvey, K.S., M. K. Young, T. M. Wilcox, D.M. Bingham, K. L. Pilgrim, and M. K. Schwartz. 2016. Patterns of hybridization among Cutthroat Trout and Rainbow Trout in Northern Rocky Mountain streams. *Ecology and Evolution* 6 (3): 688–706.
- Moyle, P.B. 2002. *Inland fishes of California*. University of California Press, Berkeley.
- Moyle, P.B., T. Light. 1996. Biological invasions of fresh water: Empirical rules and assembly theory. *Biological Conservation*. 78:149-161.
- Moyle, P.B., M.P. Marchetti. 2006. Predicting Invasion Success: Freshwater Fishes in California as a Model. *BioScience*. 56: 515-524.
- Muhlfeld, C. C., T.E. McMahon, M.C. Boyer, R.E. Gresswell, 2009. Local-habitat, watershed and biotic factors influencing the spread of hybridization between native westslope cutthroat trout and introduced rainbow trout. *Trans. Am. Fish. Soc.* 138: 1036–1051.
- Muhlfeld, C. C., R.P. Kovach, L.A. Jones, R. Al-Chokhachy, M.C. Boyer, R.F. Leary, ...

- & F.W. Allendorf. 2014. Invasive hybridization in a threatened species is accelerated by climate change. *Nature Climate Change*, 4(7): 620.
- Mycko, S. A., Y. Kanno, and J. M. Bettinger. 2018. Using angling and electrofishing to estimate Smallmouth Bass abundance in a regulated river. *Fisheries Management and Ecology* 25:77–84.
- Nagid, E. J., T. F. Bonvechio, K. I. Bonvechio, and W. F. Porak. 2015. Suwannee Bass *Micropterus notius* Bailey and Hubbs, 1949. Pages 67–73 in M. D. Tringali, J. M. Long, T. W. Birdsong, and M. S. Allen editors. *Black bass diversity: multidisciplinary science for conservation*. American Fisheries Society, Symposium 82, Bethesda, Maryland.
- Near, T. J., Kassler, T.W., Koppelman, J.B., Dillman, C.B., Philipp, D.P. 2003. Speciation in North American black basses, *Micropterus* (Actinopterygii: Centrarchidae). *Evolution* 57:1610–1621.
- Omernik, J.M. 1987. Ecoregions of the Conterminous United States. *Annals of the Association of American Geographers*. 77: 118-125.
- Orth, D.J., T.J. Newcomb. 2002. Certainties and uncertainties in defining essential habitats for riverine smallmouth bass. *American Fisheries Society Symposium*. 31: 251-264.
- Oswald, K.J. 2007. Phylogeography and contemporary history of Redeye Bass (*Micropterus coosae*). Ph.D. Dissertation, University of South Carolina.
- Oswald, K., J.Leitner, D. Rankin, D. H. Barwick, B. Freeman, T. Greig, M. Bangs, and J. Quattro. 2015. Evolutionary genetic diversification, demography, and

- conservation of Bartram's Bass.
- Parsons, J.W. 1954. Growth and habits of Redeye Bass. *Transactions of the American Fisheries Society*. 83: 202-211.
- Peoples, B. K., & Goforth, R. 2017. Commonality in traits and hierarchical structure of vertebrate establishment success. *Diversity and Distributions*.v23: 854–862.
- Peoples, B. K., & Midway, S. R. 2018. Fishing pressure and species traits affect stream fish invasions both directly and indirectly. *Diversity and Distributions*.
- Perkin, J. S., Z. R. Shattuck, P. T. Bean, T. H. Bonner, E. Saraeva, and T. B. Hardy. 2010. Movement and microhabitat associations of Guadalupe Bass in two Texas rivers. *North American Journal of Fisheries Management* 30: 33–46.
- Peterson, D. 2015. Distribution and amount of hybridization between Shoal Bass and the invasive Spotted Bass in the lower Flint River, Georgia. Volume 82.
- Pierce, P.C. and M.J. Van Den Avyle. 1997. Hybridization between introduced Spotted Bass and Smallmouth Bass in reservoirs. *Transactions of the American Fisheries Society* 126: 939-947.
- Pipas, J.C., F.J. Bulow. 2011. Hybridization between Redeye Bass and Smallmouth Bass in Tennessee Streams. *Transactions of the American Fisheries Society*. 127: 141-146.
- Pyšek, P., and D. M. Richardson. 2010. Invasive Species, Environmental Change and Management, and Health. *Annual Review of Environment and Resources* 35: 25–55.
- Rabeni C.F. and S.P. Sowa. 1996. Integrating biological realism into habitat restoration

- and conservation strategies for small streams. *Canadian Journal of Fisheries and Aquatic Sciences*. 53(1): 252-259.
- Rahel, F.J., J.D. Olden. 2008. Assessing the Effects of Climate Change on Aquatic Invasive Species. *Conservation Biology*. 22: 521-533.
- Ramsey, J.S. 1973. The *Micropterus coosae* complex in the southeastern U.S. (Osteichthyes, Centrarchidae). *Association of Southern Biologist Bulletin*. 20:76.
- Rankin, E. T. 1986. Habitat selection by smallmouth bass in response to physical characteristics in a natural stream. *Transactions of the American Fisheries Society* 115: 322–334.
- Rhymer, J. M., and D. Simberloff. 1996. Extinction by hybridization and introgression. *Annual Review of Ecology and Systematics* 27: 83–109.
- Ricciardi, A., M. F. Hoopes, M. P. Marchetti, and J. L. Lockwood. 2013. Progress toward understanding the ecological impacts of nonnative species.” *Ecological Monographs* 83 (3): 263–82.
- Rider, S. J., and M. J. Maceina. 2015. Alabama Bass *Micropterus henshalli* Hubbs & Bailey, 1940. Pages 83–91 in M. D. Tringali, J. M. Long, T. W. Birdsong, and M. S. Allen, editors. *Black bass diversity: multidisciplinary science for conservation*. American Fisheries Society, Symposium 82, Bethesda, Maryland.
- Rosenfeld, J. 2003. Assessing the Habitat Requirements of Stream Fishes: An Overview and Evaluation of Different Approaches. *Transactions of the American Fisheries Society*. 132: 953-968.
- Ryman, N., and F. Utter. 1986. *Population genetics and fishery management*. Washington

- Seagrant Program.
- Sammons, S. M., and M. R. Goclowksi. 2012. Relations between Shoal Bass and congeneric black bass species in Georgia rivers with emphasis on movement patterns, habitat use and recruitment. Final Report to Georgia Department of Natural Resources, Social Circle.
- Sammons, S. M., K. L. Woodside, and C. J. Paxton. 2015. Shoal Bass *Micropterus cataractae* Williams & Burgess, 1999. Pages 75–81 in M. D. Tringali, J. M. Long, T. W. Birdsong, and M. S. Allen, editors. Black bass diversity: multidisciplinary science for conservation. American Fisheries Society, Symposium 82, Bethesda, Maryland.
- Saunders, R., M.A. Bozek, C.J. Edwards, M.J. Jennings, S.P. Newman. 2002. Habitat Features Affecting Smallmouth Bass *Micropterus dolomieu* Nesting Success in Four Northern Wisconsin Lakes. American Fisheries Society Symposium 31: 123-134).
- Schlosser, I.J. 1991. Stream Fish Ecology: A Landscape Perspective. *BioScience*. 41: 704-712.
- Schwartz, M.K., K.L. Pilgrim, K.S. McKelvey, E.L. Lindquist, J.J. Claar, S. Loch, L.F. Ruggiero. 2004. Hybridization Between Canada Lynx and Bobcats: Genetic Results and Management Implications. *Conservation Genetics*. 5: 349-355.
- Scott, M. C., and P. L. Angermeier. 1998. Resource use by two sympatric black basses in impounded and riverine sections of the New River, Virginia. *N. Am. J. Fish. Manage.* 18:221–235.

- Scott, M. C. and G.S. Helfman. 2001. Native invasions, homogenization, and the mismeasure of integrity of fish assemblages. *Fisheries*. 26: 6-15.
- Scribner, K.T., K.S. Page, M.L. Bartron. 2001. Hybridization in freshwater fishes: a review of case studies and cytonuclear methods of biological inference. *Reviews in Fish Biology and Fisheries*. 10:293-323.
- Simberloff, D. 1996: Hybridization between native and introduced wildlife species: importance for conservation. *Wildlife Biology* 2: 143-150.
- Splendiani, A., P. Ruggeri, M. Giovannotti, S. Pesaresi, G. Occhipinti, T. Fioravanti, ... & V.C. Barucchi. 2016. Alien brown trout invasion of the Italian peninsula: the role of geological, climate and anthropogenic factors. *Biological invasions*, 18(7): 2029-2044.
- Strong, W. A., E. J. Nagid, and T. Tuten. 2010. Observations of physical and environmental characteristics of Suwannee Bass spawning in a spring-fed Florida river. *Southeastern Naturalist* 9:699–710.
- Taylor, A. T., M. Papes, and J.M. Long. 2017. Incorporating fragmentation and non-native species into distribution models to inform fluvial fish conservation. *Conservation Biology*. 32: 171–182.
- Taylor, A.T., M.D. Tringali, P.M. O'Rourke, and J.M. Long. 2018. Shoal Bass Hybridization in the Chattahoochee River Basin near Atlanta, Georgia. *Journal of Southeastern Association of Fish and Wildlife Agencies*. 5: 1-9.
- Thurow, R.F., C. A. Dolloff, J. E. Marsden. 2013. Visual Observation of Fish and Aquatic Habitat. *Fisheries Techniques, Third Edition*.

- Todd, B.L., C.F. Rabeni. 1989. Movement and Habitat Use by Stream-Dwelling Smallmouth Bass. *Transactions of the American Fisheries Society*. 118:229-242.
- Tringali, M.D., J.M. Long, T.W. Birdsong, M.S. Allen. 2015. Black bass diversity: multidisciplinary science for conservation. American Fisheries Society, Bethesda, Maryland. Symposium 82.
- Wagner T., J.T. Deweber, J. Detar, J.A. Sweka. 2013. Landscape-scale evaluation of asymmetric interactions between brown trout and brook trout using two-species occupancy models. *Transactions of the American Fisheries Society* 142: 353–361.
- Wentworth, C. K. 1922. A Scale of Grade and Class Terms for Clastic Sediments. *The Journal of Geology*. Volume 30, no. 5. 377–92.
- Whitmore, D. H. 1983. Introgressive hybridization of Smallmouth Bass (*Micropterus dolomieu*) and Guadalupe Bass (*M. treculi*). *Copeia*. 3: 672–79.
- Wiens, J.A. 2002. Riverine landscapes: taking landscape ecology into the water. *Freshwater Biology*. 47: 501-515.
- Williamson, Mark, and Alastair Fitter. 1996. The varying success of invaders. *Ecology* 77.6: 1661-1666.
- Winemiller, K. O. 2005. Life history strategies, population regulation, and implications for fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences*, 62 (4): 872-885.
- Young, M. K., D.J. Isaak, K.S. McKelvey, T.M. Wilcox, K.L. Pilgrim, K.J. Carim, ... & M.K. Schwartz. 2016. Climate, demography, and zoogeography predict introgression thresholds in salmonid hybrid zones in Rocky Mountain streams.

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