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Understanding movement, habitat use, and habitat selection by largemouth bass (micropterus nigricans x salmoides) and Alabama Bass (micropterus henshalli) on Lake Hartwell, South Carolina

Deon Kerr
deonk@clemson.edu

UNDERSTANDING MOVMENT, HABITAT USE, AND HABITAT SELECTION BY LARGEMOUTH BASS (*MICROPTERUS NIGRICANS X SALMOIDES*) AND ALABAMA BASS (*MICROPTERUS HENSHALLI*) ON LAKE HARTWELL, SOUTH CAROLINA

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Deon Thomas Kerr

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Dr. Troy Farmer, Committee Chair

Dr. Catherine Jachowski

Mr. Jason Bettinger

ABSTRACT

Alabama Bass (*Micropterus henshalli*) were illegally introduced into the upper Savannah River Basin 15-20 years ago and have since become abundant as well as problematic ecologically. Acoustic telemetry was used to quantify diel movement, habitat use, and habitat selection of Alabama Bass and Largemouth Bass in Lake Hartwell, SC across seasons (June 2021-July 2022) with the goal of informing ongoing habitat enhancement efforts. Across all seasons, Alabama Bass conducted diel horizontal migrations from deeper offshore habitats during the day to nearshore, shallow habitats at night. Daytime Alabama Bass movement rates in offshore waters were higher than nighttime movement rates. Largemouth Bass remained in shallow, nearshore habitats during both day and night and moved less at night. When both species were nearshore at night, Alabama Bass used deeper habitats than Largemouth Bass potentially indicating habitat partitioning between species. During spring, Alabama Bass used deeper habitats compared to Largemouth Bass, suggesting differences in spawning habitats may exist. Discrete choice models revealed that Largemouth Bass had positive selection for all habitat structure classifications with the strongest odds of selecting installed woody structure during the day. Alabama Bass selection for rocky structures was highest across a diel time period while selection for installed course woody structures was weak. Our results suggest key differences in behavior and habitat use/selection of both species residing in the same system. Moreover, installed woody structures placed in shoreline habitats would likely benefit Largemouth Bass in Lake Hartwell while providing limited benefits for Alabama Bass.

DEDICATION

I dedicate this thesis to my Lord and savior Jesus Christ; may He find glory in this research of his own creation. Second, I dedicate this to my fiancé Jenna, who has always been behind me to push me to my best self. Without Jenna, I do not think I would have even pursued my passion for fish and wildlife, but she has brought out the best in me and now, I am living my dream as fish biologist.

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CHAPTER 1

EVALUATING MOVMENT AND HABITAT USE PATTERNS BY LARGEMOUTH AND ALABAMA BASS ON LAKE HARTWELL, SOUTH CAROLINA

1. Introduction

Black bass are one of the most popular freshwater sport fishes in the United States. The annual number of black bass tournaments in the United States has increased steadily over the past 4 decades with approximately 40,000 black bass tournaments held across 14 southeastern states since 2011 (Shupp, 1979; Duttweiler, 1985; Schramm et al., 1991b; Kerr and Kamke 2003; Schramm and Hunt, 2007; Driscoll et al., 2012; Driscoll and Myers, 2014). During 2007-2008, an estimated US$31 million was generated from total direct angler expenditures due to black bass fishing tournaments at Sam Rayburn Reservoir, TX (Driscoll and Myers (2014).

Ecologically, Largemouth Bass (*Micropterus nigricans*) and the closely related congener Florida Bass (*Micropterus salmoides*; Kim et al. 2022) are often the top predator in many North American aquatic systems (Howick and O'Brien, 1983). Largemouth Bass often use structural cover and vegetation for foraging opportunities and can have variable movement patterns in lakes due to macro-habitat availability (Fish & Savitz, 1983; Mesing and Wicker, 1986; Wildhaber and

Neill, 1992; Ahrenstorff et al., 2009). Lakes with sufficient amounts of littoral structural cover (dense sub-merged aquatic vegetation, woody debris, etc.) can effectively congregate Largemouth Bass closer to shore and reduce their home range sizes (Bain and Boltz, 1992; Essington and Kitchell, 1999; Sass et al., 2006a; Ahrenstorff et al., 2009). However, there is little published research that assess movement and habitat use of Largemouth Bass residing in reservoirs that have established, non-native Alabama Bass (*Micropterus henshalli*) populations.

Once believed to be a sub-species of the Northern Spotted Bass (*Micropterus punctulatus*), Alabama Bass was recognized as a distinct species of black bass in 2008 after genetic verification confirmed its close relation to the redeye bass clade and not the Northern Spotted Bass. (Baker et al., 2008; Rider and Maceina, 2015). Recent phylogenomic analyses have confirmed this status as a distinct species in the spotted bass clade and indicated the undescribed Choctaw Bass (*Micropterus cf. punctulatus*) as a sister species (Kim et al. 2022). Their native distribution resides in the Mobile River Basin which spans throughout designated parts of Alabama, Georgia, and Mississippi (Rider and Maceina, 2015). Approximately 20-25 years ago, Alabama Bass were illegally introduced into the upper Savannah River Basin and have become abundant and have hybridized with native Bartram's Bass (*Micropterus cf. coosae*) (Bangs et al. 2018). In other systems introduced Alabama Bass have been suggested to negatively impact native black bass species (Rider and Maceina 2015; Dorsey and Abney 2016). The non-native range of Alabama Bass continues to expand through unauthorized introductions, reaching as far north as the state of Virginia and as far west as California (Pierce and Van Den Avyle 1997; Barwick et al. 2006; Moyer et al. 2014). State agencies are concerned their native black bass fisheries could be negatively impacted by genetic introgression (Bangs et al. 2018) and competition (Dorsey and Abney 2016;). Although introgressive hybridization is believed to be the biggest threat Alabama

Bass pose to native black bass, there is no substantial impact on Savannah River Largemouth Bass by hybridization between the two species (Bangs et al. 2018). However, Alabama Bass can be problematic for Largemouth Bass and Florida Bass through other means including inter-specific competition. Their ability to establish and achieve high abundances may lead to resource competition between species, resulting in negative impacts (e.g., reduced condition, growth) to native Largemouth or Florida Bass. While potential competition between black species inhabiting the same system is a logical concern, more knowledge about habitat use and diel seasonal movement patterns is required to understand how Alabama Bass interact, hybridize, and, potentially, compete with native black bass species.

Alabama Bass introductions continue to occur with large-scale habitat enhancement efforts that have become common across North American reservoirs as a compensation for scarce complex structures and cover (Miranda et al. 2010). Enhancement efforts often seek to improve primary production and foraging (Prince and Maughan, 1979), as well as spawning substratum to improve natural reproduction (Bassett, 1994) and young-of-year fish survival (Wege and Anderson, 1978). In addition to improving survival and recruitment, fisheries managers implement habitat installation efforts to attract and aggregate fish, with the goal of improving angler catch rates (Harris et al, 2018). Large-scale habitat improvement projects are time-intensive and costly (Harris et al. 2018); therefore, habitat enhancement efforts that are informed by sound science should produce the most efficient use of limited resources.

The challenge management agencies face is how to enhance habitats for native black bass species without improving Alabama Bass habitats. In our specific study area, the South Carolina Department of Natural Resources (SCDNR) is enhancing Lake Hartwell’s available habitat structures with the intent of improving the Largemouth Bass fishery. Until now, the effects on both

Largemouth and Alabama Bass by this initiative has not been assessed. Our objectives were to 1) quantify diel hourly movement rates and determine if differences exist between species, time period (i.e., day vs. night), among seasons, or habitat enhancement treatments (i.e., presence/absence of installed habitats) 2) quantify habitat use (i.e., distance from shore, depth) and determine if differences exist between species, time period, or among seasons. Results of this study will fill knowledge gaps concerning Alabama Bass movement ecology and habitat use in large reservoirs with native black bass species and provide information to support management decisions regarding standardized monitoring survey designs and habitat enhancement strategies.

2. Methods

2.1 Study Area

Lake Hartwell is a large (23,000 ha), mesotrophic, man-made inland reservoir with an average depth of 14 m located in the southeastern part of the United States bordering South Carolina and Georgia. The United States Army Corps of Engineers operates the lake for municipal water allocation, flood control, hydropower production, fish and wildlife, and recreational activities. As a flood storage reservoir, Lake Hartwell is typically drawn down 2 m during late fall in preparation for winter and spring rains and has a 10.6 m conservation pool that can be drawn down during periods of drought to meet downstream water demands. As a result, Lake Hartwell can experience variable water levels across the year. The impoundment is consistently ranked among the top 25 bass fishing lakes in the southeastern United States (Bassmaster 2022) and has hosted the Bassmaster Classic tournament four times in recent years (2008, 2015, 2018 and 2022). Despite supporting a popular black bass fishery, Lake Hartwell lacks abundant submerged aquatic vegetation (SAV) and other complex habitat structures as the lake was scrubbed of timber during construction.

Beginning in 2014, the South Carolina Department of Natural Resources (SCDNR) initiated a large-scale habitat enhancement effort on Lake Hartwell. This project is the result of the 2006 settlement with Schlumberger Technology Corp. for damages to the recreational fisheries in Lake Hartwell due to PCB contamination. The habitat enhancement project received $2.8 million from the settlement. During this habitat enhancement effort, a diversity of structures including cut-cabled trees and stumps, concrete structures, riprap, and artificial fish attractors have been deployed in coves and in open water areas. Overall, the objectives of this initiative are to: 1) improve and enhance habitat structures for Largemouth Bass, 2) increase productivity of the Largemouth Bass fishery by increasing recruitment, and 3) increase angler catch rates of Largemouth Bass.

2.2 Study Design

To quantify Largemouth Bass and Alabama Bass movement rates we focused our initial effort on four study coves (Figures 1) in the Seneca River arm of the reservoir and had an average area of ~38 ha (minimum 20 ha, maximum 45 ha). Study coves that contained only natural habitat structures were classified as control coves (Coves "A" and "D") while coves with habitat enhancements were classed as treatments (Coves "B" and "C"). Treatment coves had cut-and-cabled trees, deep water rock and stump piles, and artificial fish attractors installed. Movement rates data were collected in these four coves to determine if movement rates differed between treatment and control coves. Data on Largemouth Bass and Alabama Bass depth and distance from shore was collected from the entire Seneca River arm of Lake Hartwell.

2.3 Fish Collection and Transmitter Implanting

Largemouth and Alabama Bass were collected March – June, and November of 2021 using pulsed DC boat electrofishing equipped with a Midwest Lake Electrofishing System Infinity control box (Polo, Missouri). We used morphological characteristics of adults to differentiate between Alabama and Largemouth Bass (Godbout et al. 2009). However, Bartram's Bass is another native Black Bass that occurred in the Savannah River Basin historically but have rapidly hybridized with Alabama Bass in recent years (Oswald et al. 2015). Due to this known hybridization issue, we only tagged fish that appeared to be pure Alabama Bass or Largemouth Bass based on established external morphological traits (Godbout et al. 2009). Lake Hartwell lies within the intergrade zone between the native ranges of Largemouth Bass and Florida Bass (Bailey and Hubbs 1949; Silliman et al. 2021; Kim et al. 2022) and morphological identification between Largemouth and Florida Bass is difficult, meaning the Largemouth Bass we implanted transmitters into in Lake Hartwell likely contain a mix of both Largemouth Bass and Florida Bass genes (*M. nigricans* x *M. salmoides*). We used Sonotronics®' CT-82-I (2-month battery life; 6 g), CTT-82-I (CTT) (14-month battery life; 9 g), and IBT-96-I (IBT) (9-month battery life; 4 g) (Tucson, AZ) internal acoustic transmitters to monitor fish movements. Individuals less than 380 mm in total length (TL) received an IBT transmitter while fish greater than 380 mm received either a CTT or IBT transmitter. No Largemouth or Alabama Bass smaller than 305 mm were tagged to avoid transmitters exceeding 2% of a given fish's body weight (Smircich and Kelly 2014). Transmitters used 15 different frequencies (69 – 83 kHz) that were evenly distributed among tagged individuals in each study cove to minimize detection overlap while manually tracking. Fish were immobilized using electroanesthesia delivered through our boat electrofisher with pulsed direct current (5-7 amps) (Vandergoot et al. 2011). All transmitters were surgically implanted into the peritoneal cavity via a small abdominal incision posterior to the pelvic girdle and anterior to the anal vent.

An external dart tag (FT-1-94 Dart Tag, Floy Tag & Manufacturing, INC., Seattle, WA) was inserted just below the dorsal fin and possessed a unique identification number and the Clemson University Aquatic Research Laboratory's phone number so that anglers could report a captured fish as well as its fate (released or harvested). Lastly, a fin-clip was taken from the pelvic fin and placed in small plastic vials filled with 95% proof Ethanol to verify and compare species field identifications with genetic markers (Oswald et al. 2015). Following surgery, each individual was placed and remained in an aerated recovery tank for 15 minutes, monitored for signs of recovery (e.g., upright orientation, regular gill movement) and then released at the at the back of the cove the fish were captured from. All procedures for surgery, implanting, recovery, and release followed Clemson University Animal Use Protocol 2021-018.

2.4 Manual Tracking

Active tracking began in June 2021 and continued monthly until July 2022. To avoid any implanting effects on movement behavior, active tracking began > 7 d post-implantation to allow tagged fish sufficient time to resume normal behavior (Harris et al. 2018). Two diel tracking events were conducted monthly (day/night): movement rates data were collected only within the four coves to determine if they differed between treatment and control coves. Data on Largemouth and Alabama Bass depth and distance from shore was collected from the entire Seneca River arm of Lake Hartwell during the habitat use tracking event.

2.5 Movement Rate Tracking

Diel tracking events that assessed movement rates alternated each month between control and treatment coves so that diel hourly movement rates were quantified in both treatment and control covers throughout the 13-month period season. To calculate movement rates for daytime we considered only movement data collected one hour after sunrise and no later than an hour before sunset. Nighttime movement rate data was collected one hour after sunset and no later than one hour before sunrise the next day. Our methods for 24-hour tracking are similar to previous studies quantifying diel movement rates (Harris et al. 2018; Edge et al. 2020). The goal was to have a maximum subset of eight individuals per 24-hour period each month evenly split between Alabama Bass and Largemouth Bass, however, in some months due to low numbers of implanted fish present in our control and treatment coves, we did not meet this objective. During each monthly movement rate event, our goal was to relocate each selected fish at least 3 times during the day or night period to quantify hourly movement rates.

We used Sonotronics®' USR-14 Ultrasonic receiver (Tucson, AZ) equipped with a directional hydrophone to relocate a random sub-set of fish over a 24-hour period to get day and nighttime movement rates. Each study cove had 1-12 (based on cove size and shape) fixed listening locations (Figure 1). At the beginning of each tracking month, the starting listening location was randomly selected from there, we began listening for tagged fish at the starting location and proceeded to listen at each station until all listening stations were used or until we reached our target of number of fish detected. After detecting a tagged individual, an electric trolling motor was used to move toward the direction of the signal until directly on top of it (signal strength equally loud in 360° and further increases when the directional hydrophone points straight down) at which point the fish's position was recorded with a global navigation satellite system (GNSS) Arrow 100 unit by Eos (Terrebonne QC, Canada). The Arrow 100 unit collected point locations at sub-meter accuracy and was paired with Esri's (Redlands, California) ArcGIS Collector via mobile app to mark individual locations. Each selected Alabama and Largemouth Bass was located once every 1-2 hours to get at least three relocations for each individual during day and night. Some fish moved out of the study cove during tracking events, when this occurred, a new individual was selected using the previously defined methods. Any fish that had a minimum of three relocations during a single day or night tracking event was included in analysis. Hourly movement rates were quantified by measuring the distance to the nearest m between subsequent locations. All distances were measured on Esri® Collector mobile app.

2.6 Habitat Use Tracking

Habitat variables were recorded during each monthly diel habitat use tracking event. Habitat use tracking events covered approximately 28 km in linear distance across Lake Hartwell and took approximately 10 days each month to complete. The same methods for relocating an individual during the movement rate tracking event were applied during habitat use tracking events. At each fish location we recorded depth (m) with a depthfinder (Fishfinder®, Lowrance), distance to nearest (m) from shore with a range finder (Aculon A11, Nikon) and the GPS location of the fish.

2.7 Statistical Analysis

Generalized linear mixed effect models (GLMMs) were used to determine if movement rate, distance from shore, and depth differed by species, season, time period, and (for movement rate only) habitat enhancement treatments. Season for this study was defined as 3-month intervals where March – May is spring, June – August is summer, September – November is fall, and December – February is winter. The diel movement rate GLMM used the following fixed effects: species (ALB and LMB), time period, season, and habitat enhancement (coves with [treatment] or without [control] habitat enhancements) while interaction effects were included for species X time period, species X season, and species X habitat enhancement. Depth and distance from shore

GLMMs used the same main fixed effects and interactions, without the habitat enhancement parameter. All GLMMs included a random intercept for each unique individual, to account for non-independence due to multiple observations of the same fish. and a Gaussian family and log-link function; significant parameters were those with 95% confidence intervals that did not overlap zero. A post-hoc analysis using the "lsmeans" package (RStudio) was used to examine pairwise comparisons between all levels of significant main effects and interactions to determine if least-square means were significantly different from zero. Tukey's HSD (or Tukey multiple comparison test) was applied to correct all family-wise error rates for each multiple comparison. All statistical analyses were completed in R version 3.3.2 (R Core Team, 2021) and used the package "glmmTMB" (Brooks et al. 2017).

3. Results

We implanted transmitters into 111 total fish across all four study sites (control and treatment coves); 16 Largemouth (4 coves x 16 fish) (n = 64) and 11 Alabama Bass in each cove (4 coves x 11 fish) (n = 44) as well as three additional tags for Largemouth Bass in cove B for a total of 67 tagged Largemouth Bass. Additional tagged fish that were not randomly selected for this movement study were part of a complimentary habitat selection study, results of which are reported elsewhere (Kerr 2022). There was a total of 337 hourly observations for Largemouth Bass and 245 for Alabama Bass, which translate to a total of 273 Largemouth Bass and 203 Alabama Bass hourly movement rate measurements (Table 2). Ten Alabama Bass and five Largemouth Bass suffered from mortality/tag expulsion. Eight of the individuals with confirmed mortality/tag expulsion were relocated and included in our analysis before being listed as a mortality/tag expulsion.

3.1 Movement Rate

Across all seasons and time periods, species had a moderate effect on movement rates (Figure 2A), with Alabama Bass movements being 40% higher than Largemouth Bass (Figure 3B). Time period had a strong effect on movement rates (Figure 2A). Across all seasons, Alabama Bass movements rate during the day was 2.0 higher than movement rates during the night. Similarly, Largemouth Bass movement rates during the day were 81% times less compared to night (Figure 3A). Across diel time periods for both black bass species, movement rates during the spring (least-square mean = 27.5 m/h) and winter (least-square mean = 10.8 m/h) were lower than those observed during the summer (least-square means = 42.5 m/h) and fall (least-square means = 42.5 m/h) which were approximately 1.0 - 3.0 times higher than average spring and winter movement rates. There was also a significant species X season interaction effect on movement rate (Figure 2A), indicating that the effect of season on movement rate differed by species. Seasonal patterns in movement rates differed between Largemouth Bass and Alabama Bass the most during spring. During spring, Alabama Bass movement rates were low and similar to those observed during winter for this species (Figure 3B). Conversely, Largemouth Bass movements rates during spring were 8.0 times higher than Largemouth Bass movements during winter (Figure 3B).

3.2 Distance from Shore

Alabama Bass and Largemouth Bass used habitats that differed in distance from shore (Figure 2B) with the average distance for Alabama Bass (least-square mean = 49.6 m) being 51% greater than Largemouth Bass (least-square mean = 29.2 m) (Figure 4B). Time period strongly effected Alabama Bass distance from shore (Figure 2B) as they were further from shore than Largemouth Bass during the day and moved closer to the shoreline at night (Figure 4A). On average, Alabama Bass (least-square mean = 57.0 m) were double the distance from shore during the day compared Largemouth Bass (least-square mean = 28.5 m) (Figure 4A). Spring (least-square mean = 21.7 m) and winter (least-square mean = 31 m) had strong effects on distance from shore (Figure 2B) and the average for spring compared to fall was 2.25 times lower while winter was 64% less than fall across species.

3.3 Depth

Overall, species had a strong effect on depth use (Figure 2C) with Alabama Bass occupied depths (least-square mean = 5.0 m) being 66% deeper compared to Largemouth (least-square mean = 3.1) (Figure 5B). Depth use for both black bass species was strongly affected by time period (Figure 2C), with deeper depths used during day and shallower depths used during night (Figure 5A). The strength of the time period effect on depth use differed by species (Figure 2C). Mean depth use for Alabama Bass during the day was 2 times higher than at night, while Largemouth Bass mean depth use during the day was only 33% greater than night (Figure 5A). Both spring (least-square mean across species = 2.5 m) and winter (least-square mean across species = 4.1 m) had strong effects on depth use (Figure 2C). Seasons spring, summer, and fall had strong species-specific differences in average depth use, where Alabama Bass used depths approximately twice as deep than Largemouth Bass in each of these seasons (Figure 5B). Depth use during winter was similar between species (Figure 5B).

4. Discussion

4.1 Movement Rate

After accounting for time period, seasonal, and treatment effects, mean hourly movement rates differed moderately by species with Alabama Bass having higher movements than Largemouth Bass. Time period had an effect on both species movements patterns, as hourly movement rates were greatest during the day. Past studies assessing diel movements of black bass have suggested similar diel effects on movement rates, where activity in Largemouth and Alabama Bass significantly decreased at night (Sammons et al. 2003; Hunter and Maceina, 2008; Goclowski et al. 2013). Largemouth Bass movements in large reservoirs can be heavily influenced by high densities of structural cover and prey availability. For example, Ahrenstorff et al. (2009) states that home range sizes and movements by Largemouth Bass can be reduced in reservoirs with higher densities of complex woody habitat structures and vegetation. Given this conclusion, we expected that movement rates in our treatment coves, which contained a diversity of habitat enhancements might be lower compared to study coves. However, there was no observed effect of habitat enhancement treatment on movement rates in Lake Hartwell. This may suggest that densities of habitat enhancements were too low to affect movement rates in Lake Hartwell coves or that other factors besides habitat availability such as prey availability, might be influencing movement rates.

A significant interaction indicated that Largemouth Bass had greater hourly movements than Alabama Bass during spring. Despite the significant interaction, our post-hoc analysis of least-square means found no significant differences in Largemouth Bass movements during the spring, although average movement rates of Alabama Bass were approximately 40% higher compared to Largemouth Bass during the spring. Alabama Bass had significantly higher movement rates during fall and summer compared to spring and winter. Previous studies assessing seasonal trends in black bass movement found that Largemouth, Alabama, and Spotted Bass were least active during colder months (November-February) compared to warmer months (May-October). (Warden and Lorio, 1975; Mesing and Wicker, 1986; Horton and Guy, 2002; Sammons and Maceina, 2005; Hunter and Maceina, 2008). Our results also suggest higher movement rates during warmer seasons, with Alabama Bass movement rates being highest when temperatures exceeded 20ºC in Lake Hartwell (June-October). Notably, Alabama Bass had a significant reduction in movements during spring. This could indicate that Largemouth Bass and Alabama Bas have different thermal optima or that Alabama Bass have spawning behavior movements that differ from Largemouth Bass. Additional research would be required to test these hypotheses.

4.2 Habitat Use

Habitat use differed between day and night periods for Alabama and Largemouth Bass. Alabama Bass were observed further from shore and occupying deeper waters than Largemouth Bass during the day. Moreover, Alabama Bass were closer to shore at night than during the day. Diel habitat shifts such as vertical or horizontal migrations are a common phenomenon across aquatic taxa that has frequently been documented in marine and freshwater environments (Hasler and Villemonte 1953; Zaret and Suffern 1976; Axenrot et al. 2004; Mehner et al. 2007; Muska et al. 2013). Previous studies have documented diel horizontal migrations of larger piscivorous fishes from pelagic, offshore habitats during the day to shallow, littoral habitats at night (Gliwicz et al. 2006; Vasek et al. 2009; Rıha et al. 2011; Muska et al. 2013). This habitat shift by visual predators during night is likely influenced by low ambient light intensity as an energy saving strategy, when foraging offshore becomes more inefficient (Hasler and Villemonte 1953; Imbrock et al. 1996; Cech et al. 2009). In our specific study area, diel horizontal shifts by Alabama Bass are likely influenced by this energy-saving forage strategy, explaining the change in distance from shore during the day and night. Alabama Bass foraging on large schools of prey fish (e.g., Gizzard Shad, Threadfin Shad, and Blueback Herring) were often observed during daytime tracking events (Deon Kerr personal observation). Diel horizontal migration can also explain observed differences in diel depth use. As fish move closer to shore at night for foraging purposes (Muska et al. 2013), depth use is likely to decrease as well. Although Alabama Bass were observed occupying similar distances from shore as Largemouth Bass at night, their depth use was significantly greater than

Largemouth Bass. This could be due to an overall deep-water preference by this species as identified by Rider and Maceina (2015) resulting in habitat partitioning to reduce competition as observed for other piscivorous fishes in large reservoirs (Westerlin et al. 2022). This may also explain why Largemouth Bass length-at-age was not negatively impacted in some reservoirs that Alabama Bass have established in (Dorsey and Abney 2016). However, declines in overall Largemouth Bass abundance have been observed following Alabama Bass introductions (Dorsey and Abney 2016), suggesting Alabama Bass may have a competitive advantage in deeper, offshore areas, limiting Largemouth Bass to nearshore habitats.

Seasonal differences in depth and distance from shore between species during the spring, summer, and fall seasons were detected. There are few studies that describes Alabama Bass habitat preferences in large water body systems. Rider and Maceina (2015) describe Alabama Bass as a species that prefers to use deeper waters in reservoirs in comparison to Largemouth Bass. Significant variations in depth use among all four seasons by Largemouth and Alabama Bass is similar to previous studies. Stewig et al. (2004) observed Alabama Bass inhabiting deeper waters than Largemouth Bass in the Coosa River, AL. Hunter and Maceina (2008) had similar findings, where they also found Alabama Bass in deeper waters compared to Largemouth Bass. Reduced depth use and distance from shore during spring in relation to summer and fall suggests influence by the spring spawning season, where Largemouth and Alabama Bass migrate closer to shore to use shallower waters. Even so, both species move nearshore to spawn during spring and there were species-specific differences detected. This evidence of habitat partitioning in depth use between Largemouth and Alabama Bass may be a key mechanism explaining low rates of hybridization between both species. Increases in both habitat variables during the warmer months (i.e., summer and fall) could be due to shifts in forage strategy. During these two seasons, freshwater fish in temperate regions are typically at their peak for activity and predator-prey interactions (Riha et al. 2015) combined with low densities of structural cover (Ahrenstorff et al. 2009) have shown to affect species foraging behavior of piscivores. Given that Lake Hartwell has low densities of complex structures combined with high abundance of Clupeids, Largemouth and Alabama Bass may frequently use pelagic zones during fall and summer while foraging on pelagic prey species.

4.3 Management Implications

Our findings have implications for multiple management activities including ongoing habitat enhancement efforts in large, southeastern reservoirs and designing appropriate boat electrofishing and other monitoring surveys for studying Alabama Bass. Given the diel movement patterns and depth occupied by Alabama Bass, this species may not be vulnerable to daytime boat electrofishing surveys. Typically, management agencies conduct boat electrofishing surveys for black bass during daylight hours. However, our results suggest boat electrofishing sampling for Alabama Bass may need to occur at night and during the spring to effectively sample Alabama Bass in large oligotrophic reservoirs such as Lake Hartwell. Additionally, our work provides quantitative estimates of both the depths and distances from shore used by Largemouth Bass and Alabama Bass so that habitat enhancement efforts can target areas that will provide the greatest benefit to Largemouth Bass while minimizing benefits for Alabama Bass. Management agencies should place complex habitat structures in shallower waters (< 4 m) and closer (< 35 m) to shore to benefit Largemouth Bass over Alabama Bass. Overall, results from this study should help improve sampling efficiency and the effectiveness of habitat enhancement efforts aimed at benefiting native black bass fisheries in large, freshwater reservoirs.

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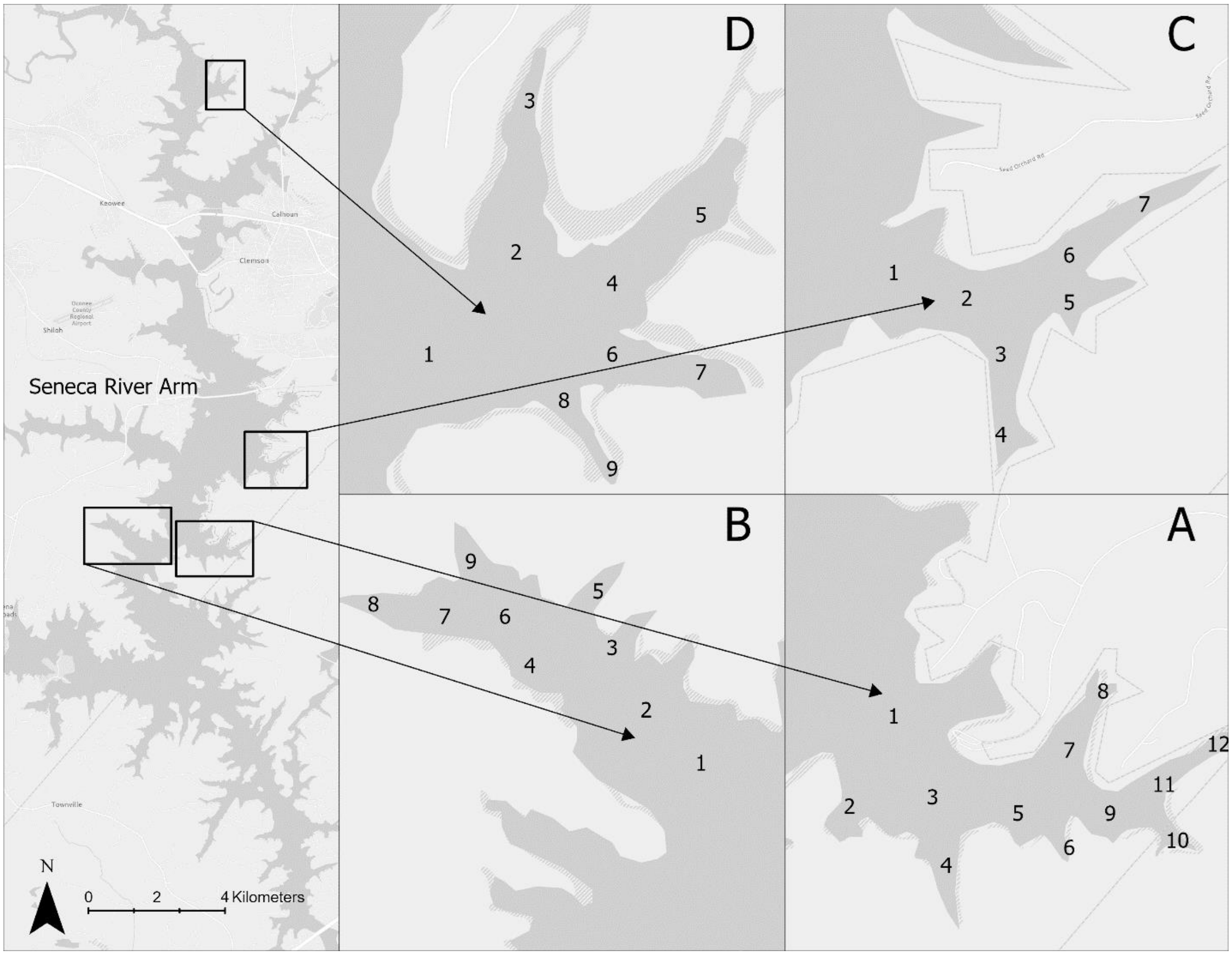


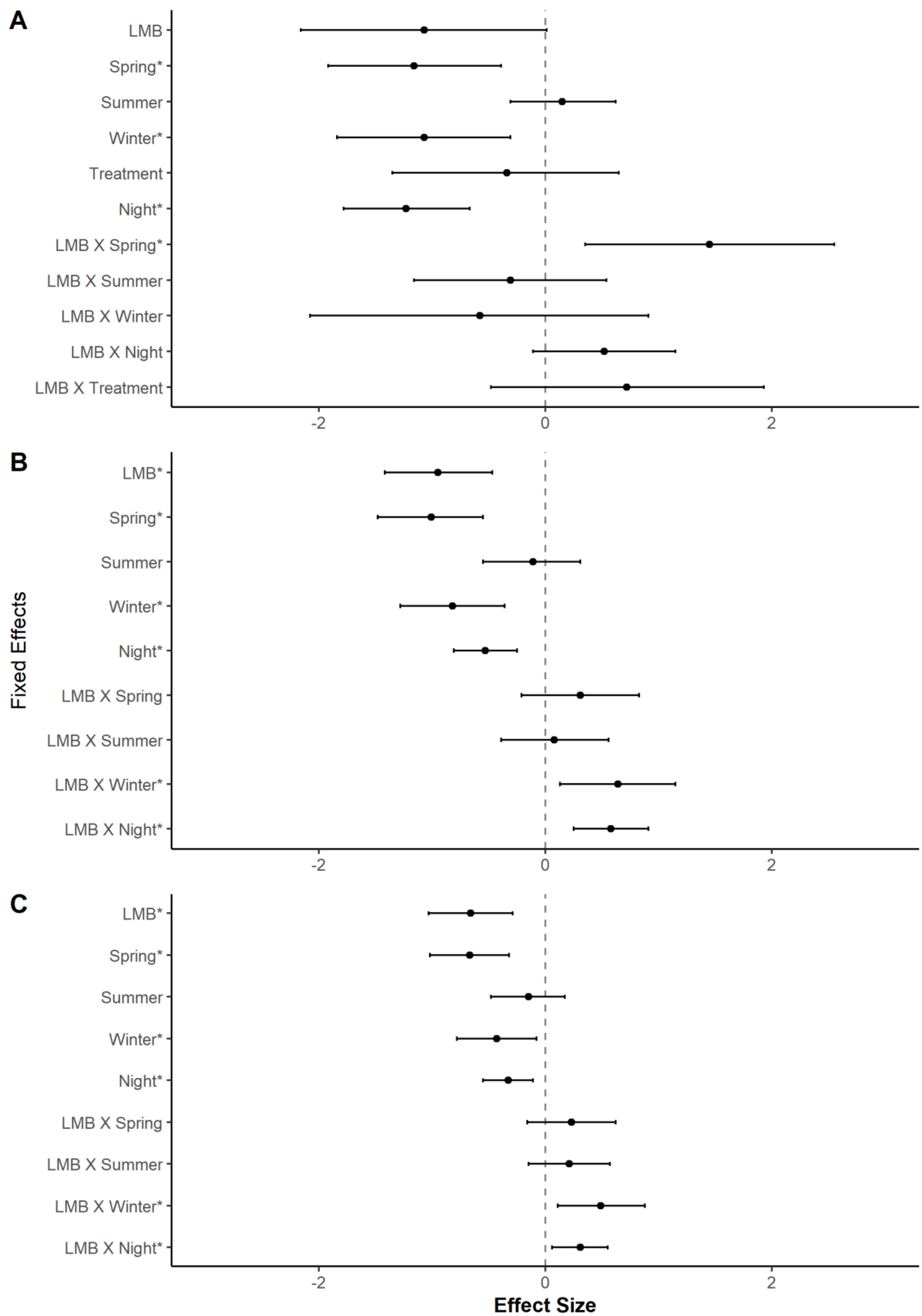
Figure 1. Geographic reference of the Seneca River arm along with the relation of all four study coves (A, B, C, and D) and their listening stations (1-12) used for diel movement rate tracking.

Table 1. Total number of Largemouth Bass and Alabama Bass tagged with acoustic transmitters and the mean, minimum, and maximum total length (TL; mm) are provided for fish tagged in each cove in Lake Hartwell, SC during 2021.

Cove	Habitat Enhancement	Species	N tagged	Mean TL (mm)	Minimum TL (mm)	Maximum TL (mm)
A	Control	Largemouth Bass	16	385	303	490
A	Control	Alabama Bass	11	388	333	439
B	Treatment	Largemouth Bass	19	393	325	560
B	Treatment	Alabama Bass	11	397	307	413
C	Treatment	Largemouth Bass	16	384	375	555
C	Treatment	Alabama Bass	11	373	310	478
D	Control	Largemouth Bass	16	428	329	600
D	Control	Alabama Bass	11	338	312	363

Table 2. Number of quantified hourly diel movment rates for Largemouth and Alabama Bass in control (C) and treatment coves (T) across all seasons (summer 2021 - spring 2022)

	Season	Day (C)	Day (T)	Night (C)	Night (T)
LMB	Spring	19	15	13	18
	Summer	26	20	32	12
	Fall	14	15	14	27
	Winter	10	18	6	14
ALB	Spring	10	20	10	18
	Summer	13	11	15	7
	Fall	14	10	14	14
	Winter	9	18	6	14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Spring*
Summer
Winter*
Treatment
Night*
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LMB X Winter
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Winter*
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LMB X Summer
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LMB X Night*
Fixed Effects
Effect Size

Figure 2. Parameter estimates from generalized linear mixed models (GLMM) with associated 95% confidence intervals for all main effects and interactions testing for significant effects of species (Alabama Bass, Largemouth Bass), season (spring, summer, fall, winter), time period (day, night) and interactions on diel movement rate (A), distance from shore (B), and depth use (C) in Lake Hartwell, SC during 2021-2022.

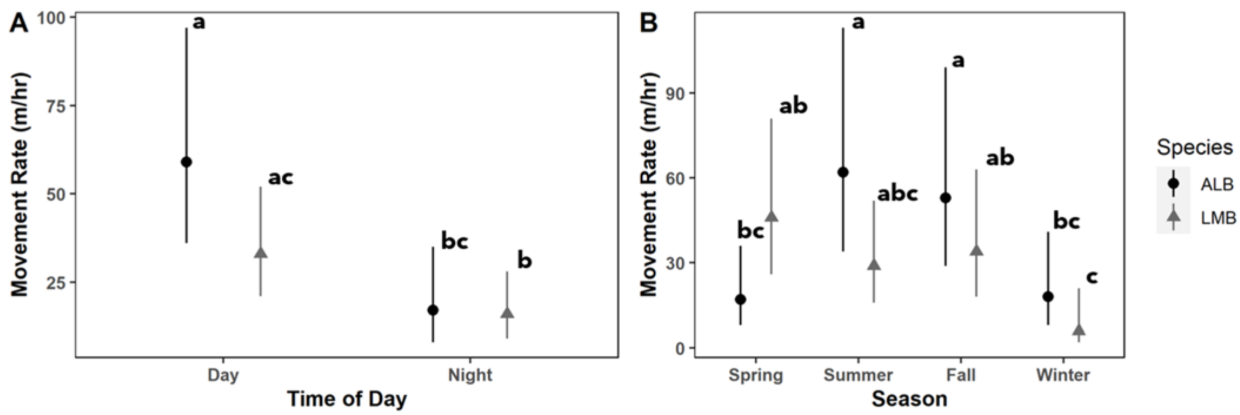

Figure 3. The least-square mean movement rate (m hr^{-1}) ± 95% CIs for day and night as well as all diel movement rates recorded in each season over the 13-month study period (June 2021 – July 2022) for Largemouth and Alabama Bass. Lowercase letters indicate least-square means that were significantly different from one another using Tukey's honest significant difference test.

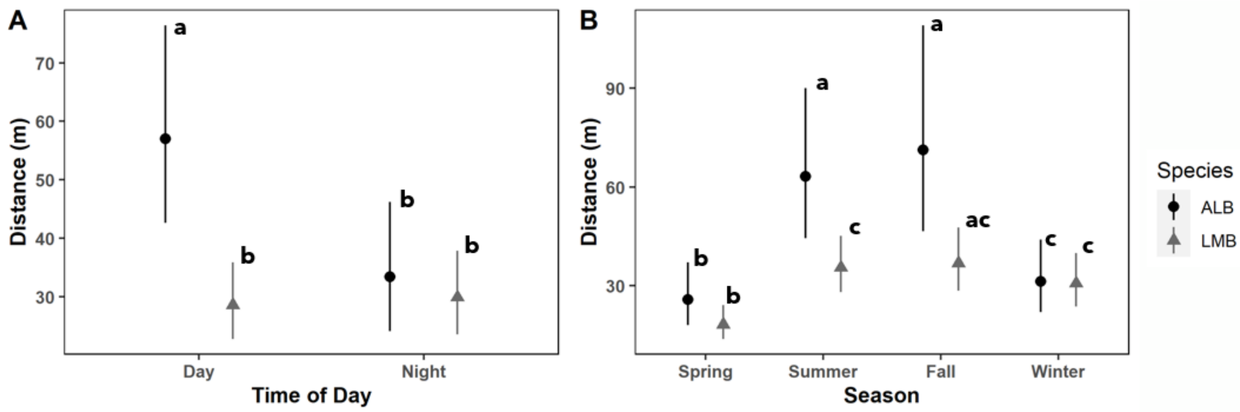

Figure 4. The least-square means (± 95% CI) for distance from shore (m) by time period and all diel habitat use measurements by season across the same 13-month period (June 2012 – July 2022) for both Largemouth and Alabama Bass. Lowercase letters indicate least-square means that were significantly different from one another using Tukey's honest significant difference test.

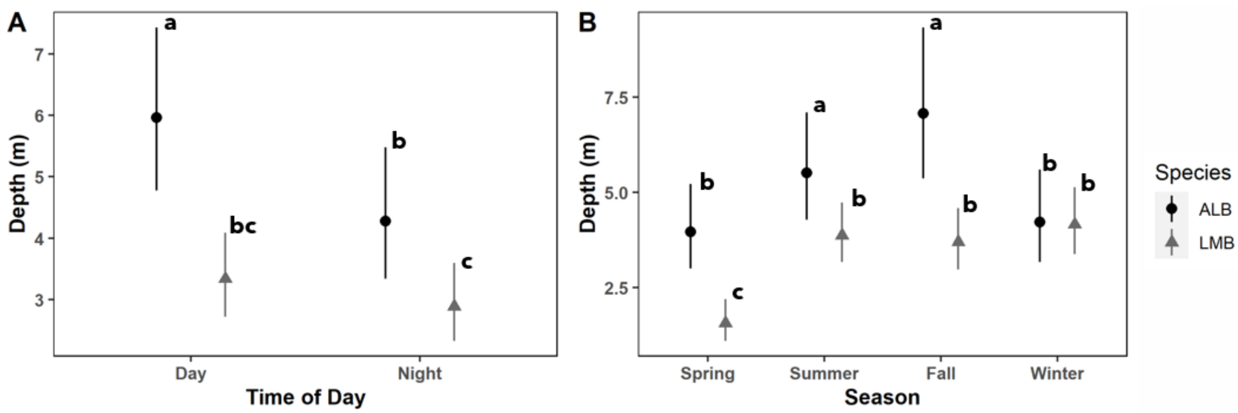

Figure 5. The least-square means (± 95% CI) for distance from shore (m) by time period and all diel habitat use measurements by season across the same 13-month period (June 2012 – July 2022) for both Largemouth and Alabama Bass. Lowercase letters indicate least-square means that were significantly different from one another using Tukey's honest significant difference test.

CHAPTER 2

ASSESSING HABITAT SELECTION OF LARGEMOUTH BASS AND ALABAMA BASS ON LAKE HARTWELL, SOUTH CAROLINA

1. Introduction

North American reservoirs are comparatively new additions to the landscape and support highly productive aquatic ecosystems within their impoundment (Pegg and Chick 2010). Construction of these massive hydrological projects in North America peaked during the mid-20th century (Miranda et al. 2010; NID, 2008) and effectively ended by the end of the 20th century, although large reservoirs continue to be constructed and planned in South America, Asia, Africa, and western Europe into present day (Zarfl et al. 2014). The United States is estimated to have over a thousand large reservoirs (> 200 ha) that were created during this period and an estimated 21 million anglers that fish them across the country (Miranda et al. 2010).

Aquatic habitats for fish in large reservoirs are diverse and differ in their habitat composition and degradation patterns due to regional topography, geomorphology, watershed characteristics, reservoir age, and construction practices (Wetzel 1990). Despite providing a vast aquatic environment, many large reservoirs may lack diverse habitats including complex structures or sufficient cover needed for fish to complete their life history activities. Absence of diverse habitats can result from various factors including, timber removal during construction, fluctuating water levels from hydroelectric damming, reservoir aging, decomposition, and sedimentation (Miranda et al. 2010; Harris et al. 2018). Suitable habitat structures provide fish with numerous benefits (e.g., refuge from predation, foraging and spawning habitats) associated with increased fitness and are a necessary component needed to sustain a healthy ecosystem.

To compensate for scarce complex structures and cover, habitat enhancement efforts have become common across North America reservoirs (Miranda et al. 2010). Enhancement efforts often seek to augment primary production and foraging (Prince and Maughan, 1979), as well as spawning substratum to improve natural reproduction (Bassett, 1994) and young-of-year fish survival (Wege and Anderson, 1979). In addition to improving survival and recruitment, fisheries managers often implement habitat installation efforts to attract and aggregate fish, with the goal of improving angler catch rates (Harris et al, 2018). According to Harris et al. (2018), large-scale habitat improvement projects are time-intensive and costly; therefore, habitat enhancement efforts that are informed by sound science should produce the most efficient use of limited resources.

Much research has focused on the importance of structural cover as a component of fish habitat (Barwick et al. 2004). Complex structures such as a submerged tree or mossback artificial fish attractors, consist of large surface areas and many different connected parts defining its structure's complexity (Gratwicke and Speight 2005). Complex structures and cover can provide fish, benefits that contribute to their survival and life cycle. Individuals may use these structures to seek refuge from predation or, on the contrary, provide predators ideal foraging opportunities (Glass 1971; Savino and Stein 1982; Werner et al. 1983). Furthermore, abundant complex structures provide many species with suitable nursery habitats, augment survival, and enhance growth (Barwick et al. 2004). However, many of these benefits vary by season in aquatic systems, including reservoirs (Schlagenhaft and Murphy 1985). Additionally, removal of complex structures, such as coarse woody debris, can impose negative effects on fish populations (Gaeta et al. 2014). For example, Gaeta et al. (2014) found that when coarse woody debris was removed from small Wisconsin lakes due to water level fluctuation periods, bass growth rates declined. Clearly, complex structures are important for black bass species. The challenge management agencies now face in recently invaded systems with Alabama Bass is how to enhance habitats for native black bass species without improving Alabama Bass habitats.

Most historical studies evaluating habitat installations have focused on habitat use, but a focus on habitat selection would provide for more useful information for selecting structures and placement of structures. Allen et al. (2014) evaluated Largemouth Bass (*Micropterus salmoides salmoides*) habitat use on Table Rock Lake, Missouri and found that Largemouth Bass used all structure types (cedar, pine, hardwoods, stumps, and rocks) but were unable to determine if any of these structures were preferentially selected. Harris et al. (2018), quantified Largemouth Bass habitat selection on the same lake and determined that boat docks were selected at twice the rate of other structures and that installed woody habitats were selected at the same rates compared to naturally occurring woody habitats. Measuring habitat selection takes far more effort than it does to assess habitat use, however the results can be far more informative.

Largemouth Bass are a popular sport fish in North America, drawing much attention from anglers and fisheries managers. There are three black bass species that reside in Lake Hartwell, two native species, Largemouth Bass and Bartram's Bass (*Micropterus sp. cf. cataractae*) and non-native Alabama Bass. Alabama Bass were introduced by illegal unauthorized stockings into the Savannah River approximately 20-25 years ago and have since become the most caught sport fish in the majority of Savannah River reservoirs (Bangs et al. 2018). Additionally, Alabama Bass appears to have eliminated pure Bartram's Bass from several Savannah River reservoirs via genetic introgression (Oswald et al. 2016) and may also compete with Largemouth Bass as previously documented in other systems (Dorsey and Abney 2016). As such, Alabama Bass are viewed as a nuisance species within the Savannah River Basin (Oswald et al. 2016).

The goal of this study was to determine if differences in habitat selection existed between two, potentially competing, black bass species. More specifically, our primary objective was to quantify 3rd order habitat selection (selection of various habitat patches within the home range; Johnson 1980) for native and non-native black bass in a large, man-made, mesotrophic reservoir in the southeastern part United States during the day and night. Both used and available habitats were quantified for native Largemouth Bass (*Micropterus nigricans*; Kim et al. 2022) and non-native Alabama Bass (*Micropterus henshalli*) in Lake Hartwell, South Carolina. Such differences may inform ongoing habitat enhancement efforts in southeastern reservoirs containing both black bass species so habitat enhancement efforts provide the greatest benefits possible for native Largemouth Bass while minimizing benefits for non-native Alabama Bass.

2. Methods

2.1 Study Area

Lake Hartwell is a large, man-made impoundment (23,000 ha) located in the southeastern part of the United States, bordering both South Carolina and Georgia. The lake was formed from a hydroelectric dam 11 km below the point where the Savannah, Seneca, and Tugaloo Rivers join. At the time of its construction, much of the natural woody structure within the reservoir basin were removed. This basin-clearing activity along with natural decomposition of remaining woody structures (Barwick et al. 2004) has resulted in low densities of complex habitat structures present in the lake today. Additionally, the combination of a mostly clay bottom, mesotrophic environment, and fluctuating water levels due to a large conservation storage pool (35 ft of lake level elevation designated by the US Army Corps of Engineers) contribute to Lake Hartwell's low abundance of submerged aquatic vegetation. Contrary to the low density of complex structures, Lake Hartwell has hosted numerous high profile black bass tournaments, including the Bassmaster Classic four times since 2008.

Adequate complex structures such as coarse woody habitat have been shown to concentrate Largemouth Bass in available habitat and creating a focal point for predator and prey interactions (Ahrenstorff et al. 2009, Sass et al. 2012). Aggregations surrounding complex habitat can result in increased angler catch rates (Tuggend et al. 2011) although this is not always the case (Allen et al. 2003). While lacking in available habitat but still supporting a popular black bass fishery, SCDNR initiated a habitat enhancement initiative for Lake Hartwell in 2014 with the goal of 1) improving and enhancing habitat structures for Largemouth Bass, 2) increase productivity of the Largemouth Bass fishery by increasing recruitment, and 3) increase angler catch rates of Largemouth Bass (see Kerr et al. 2022 for specific details).

2.2 Habitat Selection Tracking

Largemouth and Alabama Bass had acoustic transmitters surgically implanted (tagged) within them for active tracking (see Kerr et al. 2022a for descriptive methods on acoustic tagging). Tracking for bass began in June (2021) and concluded in July (2022) totaling 13-months of diel data collection. Before commencing any habitat selection tracking for the month, a 24-hour movement rate active tracking event was necessary for quantifying the distribution of day and night movement rates. The ultimate goal for habitat selection tracking was to relocate every tagged fish across a diel period (day/night) throughout the range of the Seneca River arm and assess used and available habitat. Following Harris et al. (2013)'s active tracking methods for habitat selection, monthly individual relocations occurred during both day and night periods. Daytime tracking events began one hour after sunrise and lasted no later than one hour before sunset. Conversely, night tracking events began one hour after sunset and concluded no later than one hour before sunrise. The methods used for relocating a detected fish for movement rate active tracking, were also incorporated for this tracking event (see Kerr et al. 2022a for descriptive methods on relocating detected fish). Once a detected fish was relocated, a georeference for the point-location was taken along with the used habitat variables in the area (see *Habitat Variables* below). Random available point-locations (available habitat but unused by the individual fish) were determined by a random process that included previously collected information on hourly movement rates for each species. This was accomplished by randomly drawing three values from the distribution of diel movement rate data collected from the previous and current month for each species. Movement rates were multiplied by the number of hours in each time period (which changed monthly with changes in day length) to quantify total movement within the day or night period.

Additionally, three randomly generated directional degrees were used to determine where the available point-locations reside in the lake area. The distance and directional degree were combined to determine a random, available point-location and this process was repeated three times for every used point-location. Any distance and direction that landed onto shore was reflected (180 degrees) from the shoreline back out into the water until the distance measurement was met (Harris et al. 2018). Available point-locations that were less than or equal to five meters away from the used point-location was not used and a new, available point was randomly generated.

2.3 Quantifying Manual Tracking Accuracy

Field trials with acoustic transmitters submerged in known locations were used to quantify the accuracy with which tagged fish were relocated. During field trials the manual tracking crew was blind to the known locations of acoustic tags, which were placed in known locations by an independent crew. Field trails were conducted during July 2022 on Lake Hartwell. Acoustic transmitters were placed across a range of shallow (1-4 m), medium (5-9 m), and deep depths (10-14 m) in locations unknown to the tracker and were blindly relocated. No more than 6 acoustic transmitters were placed in each depth stratum (shallow, medium, and deep) and the error of those relocations (straight line distance between known and observed locations in ArcGIS) were used to quantify accuracy. Precisions of known and relocated positions were quantified with error less than 50 cm using the Arrow 100 unit. Once accuracy was determined for each known location, linear regression was used to determine the relationship between accuracy as a function of depth. Lastly, a Cook's D test was used to determine if there were any outliers effecting the relationship between the two variables. Identifying the relationship between depth and accuracy was critical for determining the buffer size needed for classifying open water used and available points from sonar images.

2.4 Habitat Variables

A total of three (structure, depth, and distance from shoreline) macrohabitat variables at each point-location (used and available) were recorded. Visible structures were classified as follows: coarse woody structure (CWS), installed woody structure (IWS), open water (Open), rocky structure (RS), and boat docks (dock). Our rocky structure classification included both installed rock piles and natural rock outcroppings. Knowledge and GPS coordinates of SCNDR installed woody structures allowed us to separately classify naturally occurring complex woody structure (CWS) and installed woody structures (IWS), with the goal of determining if Largemouth and Alabama Bass were preferentially selecting installed over woody structures. When point-locations were in water depths that prevented visual assessment of structure, we temporarily classified structure as open water (Open). We subsequently used side scan sonar to collect digital images of physical structures at open water point-locations to visually classify submerged structures at these deeper water point-locations into the five structural classes above (additional methods detailed below). Depth was measured using a Lowrance® HOOK2 4x swivel color fishfinder with transducer (Tulsa, Oklahoma) mounted on the tracking vessel (Tracker Pro170® boat). Distance from shore during the day was measured using a (Aculon A11, Nikon®) rangefinder to the nearest 1 m. Due to light visibility limitations during night tracking events, distances from shore were instead measured using our EOS® Arrow 100 GPS antenna and GIS map to determine the distance between each point-location and the shoreline. To account for shoreline fluctuations (i.e., variable water levels throughout the year) potentially impacting distances from shore, the closest area from shore was first identified on the GIS map. Next the vessel was moved to the identified area and a GPS point was placed at that location of the vessel to determine where the actual shoreline was. After assigning a GPS point to the area, the distance between the point-location and the shoreline GPS point was measured (nearest m). Using the distance tab on the Esri® Collector app, a point line was used to determine distances from shore for used and available points at night. Moreover, substrate was also recorded but due to high uncertainty and limitations by accessibility (i.e., water was too deep) a decision was made to drop the variable from any analyses.

2.5 Classifying Structure with Sonar

When water depths prevented us from visually classifying physical structures, we used an Edgetech® 4125i side scan sonar system (i.e., tow-fish) to map the benthic zone in our study area. The tow-fish utilizes compressed high-intensity radiated pulse (CHIRP) technology in combination with high frequency acoustic waves on dual settings at 400/900khz and 600/1600khz. The high frequency range the tow-fish utilizes provided this study high-resolution images of Lake

Hartwell's benthic zone. Ensuring safe deployment and accurate images, the tow-fish was deployed at approximately 1-2 m from the hull of the boat and travel speeds were kept to a maximum of 5 mph. Sonar tows were conducted during February 2022 and covered all areas where open water point-locations were recorded.

Post-processing of side scan imagery was conducted through a combination of SonarWiz® and ArcGIS Pro® software. SonarWiz® is an open-source software product designed specifically for analyzing and decrypting sonar/side-scan imagery. The software presents a wide variety of tools the user can utilize to accomplish their objectives such as identifying river substrate, or other habitat structures (Kaeser and Litts 2013). Once our side scan images were uploaded into SonarWiz®, they were then exported into a tag image file format (TIFF). Next, TIFF images were uploaded into a topographic map in ArcGIS Pro® and projected using the WGS 1984 Web Mercator Auxiliary Sphere horizontal coordinate system (e.g., same coordinate system used for GPS point-relocations recorded during habitat selection). All point-relocations with the open water classification for structure were then converted into point features (x, y, coordinate data) and layered on top of the side-scan images for manual viewing. A buffer zone to identify the maximum extent a structure is being used was placed around the point-relocations. The buffer zone used for each point represented the accuracy quantified from field trials, so any habitat that fell within the area of the buffer was assumed used or available. Linear regression parameters calculated from your relationship between accuracy and depth was applied here to calculate the circular buffer diameter based on the depth of each point-location. After applying the buffer zone to all open water point-relocations, a visual classification was done to determine the true extent of the point (i.e., CWS, IWS, RS, dock, or open). Readers determined the identification of the open water point-relocation if a structure was found within the buffer radius. These were the final steps needed to prepare the data for analysis.

2.6 Discrete Choice Modeling

Discrete choice modeling was used to quantify 3rd order habitat selection (Jones 2001; McGarigal et al. 2016) for Largemouth and Alabama Bass. Discrete choice modeling (DCM) originated in the field of economics, however, Cooper and Millspaugh (1999) demonstrated the applicability of these models in wildlife resource selection studies. The order at which habitat selection is quantified at refers to the scale of assessment. In this study we attempt to quantify habitat selection down to the scale of microhabitat for both species of black bass (Jones 2001; Diaz et al. 2022). Economically, DCMs seek to explain the utility gain from an individual selecting a certain habitat or resource (Cooper and Millspaugh 1999). In the field of fish and wildlife science, utility gained is identified as satisfaction for an animal. Satisfaction simply refers to the assumed individual benefits from selecting one resource over another or multiple resources (i.e., increased forage, increased growth, decreased predation risk, etc.). Furthermore, DCMs do not assume that resource availability is constant over time, thus, habitat selection can be inherently expressed by defining used and available habitat for a given individual (Bonnot et al. 2011). This is made possible because a DCM takes individual variation into consideration through structuring data into a series of "choice sets"(Cooper and Millspaugh 1999). Each choice set (i.e., sample) in our analysis consisted of 1 used (i.e., bass relocation) point and 3 random available points determined to be available to an individual at a given time point. We defined availability based on point-relocations unoccupied by the individual and 5m away from the original relocation. The set of used and unused point-locations for each individual location is defined as a choice-set. As next step, hypotheses regarding variables of interest can be stated to construct candidate models.

2.7 Model Development and Fit

Four *a priori* hypotheses were formulated based on previously determined strong microhabitat preferences for both Largemouth and Alabama Bass (Table 1 and 2). Four candidate models were then fit to assess habitat selection based on these established microhabitat influences. The first candidate model assessed the influence of resource selection by *structure* (Table 1 and 2) and was built from different structure classifications (Table 3). Next, continuous variables including *distance from shore* and *depth* were used in separate models to determine the influence on habitat selection for both species of black bass (Table 1 and 2). Depth was evaluated using a quadratic form to allow the model flexibility in accommodating selection of intermediate depths. Lastly, a global model containing the combination of all microhabitat variables was fit to determine if the combination of these metrics were more important for habitat selection than just one variable (Table 1 and 2). Each of these variables used to evaluate resource selection have been previously observed to influence habitat use for either Largemouth and/or Alabama Bass (Colle et al. 1989; Rogers and Bergersen 1996; Sammons and Maceina 2005; Hunter and Maceina 2008; Rider and Maceina 2015). Candidate models for Largemouth Bass assessed resource selection for each time period individually. Due to lower sample sizes for Alabama Bass, day and night samples were pooled into a single analysis and assessed resource selection across both time periods (diel). All candidate models for Largemouth and Alabama Bass were fit in RStudio using the mlogit package.

Candidate models were ranked using Akaike's Information Criteria (AICc) which corrected for small sample sizes. Model weights (w_i) were used to determine the best fit model for Largemouth and Alabama Bass (Burnham & Anderson, 2002). After deciding the best fit model, a k-fold cross validation test (k = 5) was used to validate the top model for both species to evaluate model accuracy (Boyce, 2002). Training data utilized 80% of the top model's data, whereas the remaining 20% was used as test data for model validation. After validating the performance of the top models, the odds ratio (e^{β}) was used to express habitat selection for Largemouth and Alabama Bass (Equation 1.), where the odds ratio is interpreted as the change in odds of selection in response to a one-unit change in the level of the independent variable or, when the independent variable is categorical, the change in odds of selecting a resource in category *i* relative to a reference category All statistical analyses were conducted in RStudio (R Core Team, 2019).

3. Results

Simple linear regression was used to test if depth significantly predicted accuracy fish relocation during active tracking (Figure 1). The overall regression was statistically significant ($R^2 = 0.31$, $F_{(1, 16)} = 7.36$, $p = 0.015$) and the average buffer size across all depths recorded was 3.77 m (sd = ±1.51). In summary, as depth increased, error also increased prompting the result of a larger buffer zone as depth increased.

Throughout the entire 13-month tracking period, 496 total choice sets were used for determining habitat selection for both species of black bass on Lake Hartwell, South Carolina. There were 127 choice sets used for Alabama Bass and 369 choice sets used for Largemouth Bass. The Structure model (model 1) was the top-ranking model for Largemouth Bass day time period habitat selection ($w_i = 0.87$) (Table 4.) Model 1 was the top-ranked model for Largemouth Bass during the night ($w_i = 0.30$) and for Alabama Bass across both time periods ($w_i = 0.44$) (Table 4). Distance from shore (model 2) and Depth (model 3) were also contenders for being top models for Largemouth Bass during the night. However, both variables had small effects on resource selection. Distance from shore was also a top-ranking model for Alabama Bass but the effect on habitat selection was small as well.

3.1 Alabama Bass

Across both time periods of the day (day/night), Alabama Bass selected for all other structure classifications but avoided coarse woody structure relative to open water (Table 5). Rocky structure was strongly selected for having a three and a half-fold higher odds of selection over open water (Table 5). Alabama Bass selected for installed woody structures as well but at lower odds (Table 5.) Alabama Bass selected for open water relative to coarse woody structure in suggesting they are avoiding this structure type in Lake Hartwell. The boat dock classification was added to the installed woody structure class due to extremely low observations (n = 3).

3.2 Largemouth Bass

The structure model was ranked first for Largemouth Bass day and night habitat selection (Table 4 and 5). During the day Largemouth Bass were more likely to select all structure types over open water. Installed woody structures were most strongly selected, having a 9-fold higher odds of being selected relative to open water (Table 5). Coarse woody structure, boat docks, and rocky structures were less strongly selected than installed woody structures and selected to a similar degree as one another, having a two-to three-fold higher odds of being selected relative to open water (Table 5).

Nighttime habitat selection for structure by Largemouth Bass was similar to daytime habitat selection trends. At night all structures were selected over open water, but Largemouth Bass did not differentiate installed woody structures from other structures at night. Coarse woody structure, installed woody structure, rocky structure, and boat docks were all more than two and a half-fold odds of being selected in response to open water. In summary, Largemouth Bass exhibited strong preference for structures during both time periods (day/night) while Alabama Bass showed weaker selection of structures in response to open water availability.

K-fold cross validation concluded that the average top model prediction success score for Largemouth and Alabama Bass was 79% (sd = ±4)(Table 6). High model scores suggest all models were accurate predictors of bass habitat selection.

4. Discussion

4.1 Largemouth Bass Habitat Selection

Largemouth Bass had high preference for physical habitat structures compared to open water during the day and night in Lake Hartwell. Previous studies that assessed habitat use (Sass et al. 2012) and habitat selection (Harris et al. 2018) for Largemouth Bass highlighted the importance of complex woody structures. Our findings pertaining to Largemouth Bass structure selection are generally consistent with those previous works. Overall, strong selection for complex structures by Largemouth Bass is likely due to its life history traits such as being an ambush predator (Savino & Stein, 1982; Sass et al., 2006a). More specifically, structures can have strong effects on the ecological functions, life history, and distributions of Largemouth Bass. In lakes with high densities of coarse woody structures, Largemouth Bass were shown to have elevated growth rates and smaller home range sizes (Ahrenstorff et al. 2009). Forage strategy is also influenced by the presence of littoral structures by providing adequate ambush points for Largemouth Bass (Savino and Stein 1982; Sass et al. 2006a). Like many large reservoirs in the Piedmont physiographic region, Lake Hartwell lacks abundant submerged aquatic vegetation, which has shown to be key habitat for Largemouth Bass in other systems (Ahrenstorff et al. 2009; Sass et al. 2012; Harris et al. 2018) However, previous work has suggested that coarse woody structures in reservoirs can effectively serve as a proxy for submerged aquatic vegetation (Sass et al. 2012). Installed woody structures in this specific study were mostly composed of cut and cabled trees in the littoral zone and resulted in a much higher rate of selection during the day than night, suggesting habitat use differences. While this specific structure type was readily abundant in the Seneca River arm, the noticeable difference in selection during the day and night could be due to changes in forage tactics. Largemouth Bass are visual hunters thus affecting their ability to forage effectively on prey in low ambient light environments (McMahon and Holanov 1995). However, Howick and O'Brien (1983) found that in low-light conditions, Largemouth Bass can locate prey, such as bluegill, by detecting movement vibrations. These results suggest the reduction in selection for a using complex structures for ambush opportunities at night when light intensities are suboptimal for visual hunting.

4.2 Alabama Bass Habitat Selection

Alabama Bass exhibited avoidance for installed woody structures but had strong odds of selecting for rocky structures compared to open water. This aligns with what little information has been documented on Alabama Bass structure preferences. Rider and Maceina (2015) state that Alabama Bass were more commonly observed occupying rocky points, gravel, and cobble substrates, and were less observed to use woody structures. Alabama Bass are a species that prefers deep, clearer waters and have been shown to use areas of greater depths which might explain their lack of interest in littoral zone structures where woody and submerged vegetation are most present (Gilbert 1973; Kerr et al. 2022a). The species was also observed further from shore than Largemouth Bass which serves complimentary to its preference of open water over habitat structures. The difference in habitat preferences between the two black bass species could likely be due to forage strategy. Throughout the 13-month study period, Alabama Bass were commonly observed congregating and foraging in the pelagic zones of the lake (Deon Kerr personal observation). While structure could influence the distributions of Alabama Bass in pelagic environments, their prey might have a greater influence. Alabama Bass are defined as primarily piscivorous and shad (*Dorosoma spp*.) is the dominant fish consumed in the upper Coosa River (Gilbert 1973; Stewig and DeVries 2004) and Lewis Smith Lake, Alabama (Shepherd and Maceina 2009). In South Carolina, Lake Hartwell provides abundant Gizzard Shad (*Dorosoma cepedianum*) Threadfin Shad (*Dorosoma petenense*) and Blueback Herring (*Alosa aestivalis*) populations. Each of these species primarily use pelagic habitats which could be responsible for Alabama Bass' preference in open water in Lake Hartwell.

4.3 Management Implications

This study is the first to compare habitat selection between Largemouth and Alabama Bass in a large impoundment. Both installed and natural woody structures were identified as providing high utility (benefits) for Largemouth Bass. Installed woody structures or more specifically cut and cabled trees in the littoral zone, served as a highly valued structure to Largemouth Bass (especially during the day) followed by natural coarse woody structures at either time of the day. New or on-going habitat enhancement efforts focused on the black bass fisheries should center their efforts on installments of woody structures which should favor Largemouth Bass productivity. In reservoirs with scarce densities of submerged aquatic vegetation, complex woody structures can serve as a replacement for the missing habitat. Alabama Bass are likely to utilize rocky habitat structure installations especially when placed further away from shore in deeper environments. Agencies should be advised to not install rocky structures if their goal is not to enhance habitats selected by non-native Alabama Bass. In closing, this information will contribute to filling the knowledge gaps pertaining to Alabama Bass habitat preferences and habitat selection concerning black bass species.

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Table 1. The number and variables included for each candidate model used for discrete choice modeling. Largemouth Bass choice setes used all 4 models separately for day and night (N=8 models).

Model Number and Hypothesis	Model Structure
1. Increased selection of stucture	$= \beta 1$ (CWS) + $\beta 2$ (IWS) + $\beta 3$ (DOCK) + $\beta 4$ (RS)
2. Decreased selection of increase distance from shore	$= - \beta 1$ (DS)
3. Decreased selection of increasing depth	$= \beta 1$ (D) + $\beta 2$ (D^2)
4. Global model	$= \beta 1$ (CWS) + $\beta 2$ (IWS) + $\beta 3$ (DOCK) + $\beta 4$ (RS) + $\beta 5$ (D) + $\beta 6$ (D^2) - $\beta 7$ (DS)

Table 2. The number and variables included for each candidate model used for discrete choice modeling. For Alabama Bass, each of the 4 models was fit to choice sets for all day and night periods combined (N=4 models).

Model Number and Hypothesis	Model Structure
1. Increased selection of stucture	$= \beta1\ (CWS) + \beta2\ (IWS) + \beta3\ (RS)$
2. Decreased selection of increase distance from shore	$= -\ \beta1\ (DS)$
3. Increased selection of mid-range depth	$= \beta1\ (D) + \beta2\ (D^2)$
4. Global model	$= \beta1\ (CWS) + \beta2\ (IWS) + \beta3\ (RS) + \beta4\ (D) + \beta5\ (D^2) - \beta6\ (DS)$

Table 3. Variables used in resource selection models for Largemouth and Alabama Bass on Lake Hartwell, South Carolina.

Variable	Description	Min-Max	Mean
Depth	Water column at each point location (m)	01 - 41	5
Distance from Shore	Distance from shore at each point location (m)	01 - 656	57
CWS	Coarse Woody Structure (presence/absence)	0-1	N/A
IWS	Installed Woody Structure (presence/absence)	0-1	N/A
RS	Rocky Structure (presence/absence)	0-1	N/A
Dock	Boat Dock (presence/absence)	0-1	N/A
Open	Open Water (presence/absence)	0-1	N/A

Table 4. Akaike information criterion (AICc) adjusted for small sample size output for top ranked day and night models explaining habitat selection of Largemouth Bass (day and night) and Alabama Bass (diel) in Lake Hartwell, South Carolina, 2021-2022.

Day Period	Model No.	Log-like	K	AICc	ΔAICc	Weight
Day	1	-289.3	4	586.7	0.0	0.86
	4	-287.9	7	590.3	3.6	0.14
	2	-306.8	1	615.6	28.9	<0.001
	3	-307.0	2	618.1	31.4	<0.001
Night	1	-189.8	4	387.8	0.0	0.30
	2	-193.0	1	388.0	0.2	0.27
	4	-186.7	7	388.1	0.3	0.25
	3	-192.4	2	388.8	1.0	0.18
Diel	1	-171.1	3	348.3	0.0	0.44
	2	-173.5	1	349.0	0.7	0.31
	4	-168.8	6	350.3	2.0	0.15
	3	-173.6	2	351.3	3.0	0.10

Table 5. Parameter estimates, odds ratios, and probability of selection of structure for Alabama Bass (diel data) and Largemouth Bass (day and night). Data here is representative of the top model (1) for both species.

Species	Structure Classification	Estimate	Odds Ratio
ALB	CWS	-0.51	0.60
	IWS	0.12	1.13
	RS	1.28	3.60
LMB (day)	CWS	1.07	2.92
	IWS	2.22	9.21
	RS	0.83	2.29
	Dock	0.68	1.97
LMB (night)	CWS	1.10	2.99
	IWS	0.97	2.63
	RS	0.96	2.62
	Dock	1.08	2.94

Table 6. K-fold cross-validation model accuracy scores (% predictive success) of top models for Largemouth Bass day and night and diel Alabama Bass.

Model	Predictive Success
LMB day	76
LMB night	77
ALB diel	83

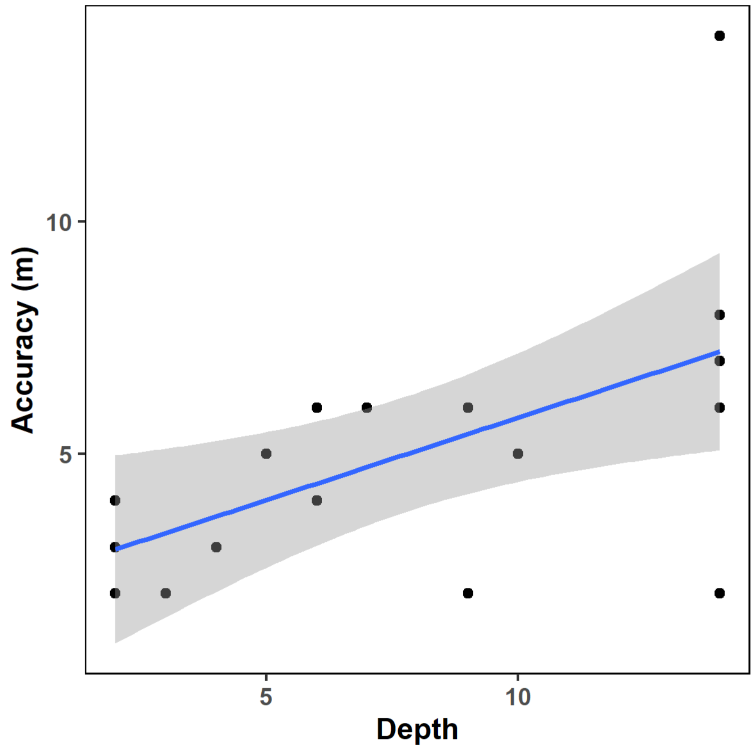

Figure 1. Linear regression determined that depth (x-axis) was a significant predictor for error (y-axis), 95%CI is located withing the shaded grey area while the blue trend line represents R^2. All data was collected during July 2022 on Lake Hartwell, SC using IBT acoustic transmitters (Sonotronics® Tuscon, AZ).

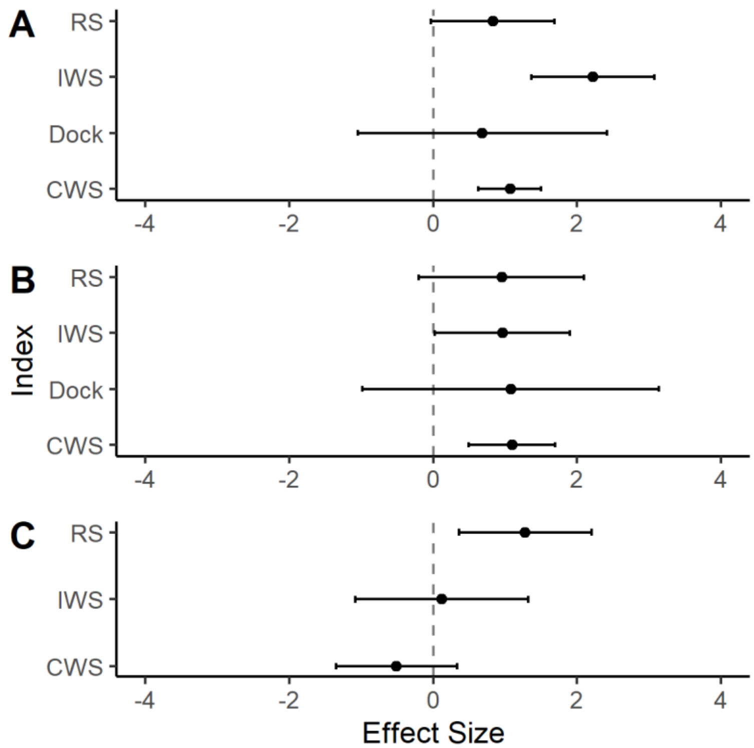

Figure 2. Parameter estimates from the top ranked discrete choice model (model 3) with associated 95% confidence intervals for Largemouth Bass day (A), night (B), and diel Alabama Bass (C) in Lake Hartwell, SC during 2021-2022.