ABSTRACT

LINCOLN, KELSEY JEAN. Potential Mechanisms Underlying a Perceived White Bass *Morone chrysops* Decline in a Southeastern Reservoir. (Under the direction of Dr. D. Derek Aday and Dr. James A. Rice).

Little is known about fundamental aspects of the life history, ecology, and population dynamics of White Bass, *Morone chrysops*, a popular sport fish in southern reservoirs. In addition, concern regarding possible declining White Bass populations in some North Carolina reservoirs has made the management of this species difficult as the mechanisms associated with these perceived declines are not well understood. Our study aimed to address these knowledge gaps through quantification of two potential mechanisms: Mortality (both fishing, *F*, and natural, *M*) and potential interactions with invasive White Perch *Morone americana*. This study also aimed to increase the general knowledge base on reservoir White Bass by examining their seasonal distribution patterns, habitat use, and spatial interactions with White Perch and by quantifying important population parameters such as growth, age structure, and population size. We used a telemetry approach to estimate the instantaneous monthly and annual *M* and *F* mortality rates of White Bass and to explore the distribution and habitat use of White Bass and White Perch. Acoustic transmitters were implanted into 50 White Bass collected at the confluence of the Haw River and Jordan Lake during their spring spawning run in 2012, 25 White Bass during spring of 2013, and 20 White Perch collected throughout the reservoir in October 2013. Tagged fish were monitored using an array of passive receivers throughout the reservoir and monthly active tracking surveys. We used stable isotope and stomach content analysis to determine the potential for competition between the two species. Fish for muscle tissue, stomach samples, and age analysis were collected via electrofishing and gillnetting in the mouth of the Haw River in spring 2013.

Additional fish were collected for diet and age analysis in January 2013 via gillnetting in the main basin of the lake. To estimate population size we tagged White Bass with Passive Integrated Transmitters in April 2011 and March and April 2012, but discontinued our efforts after 2012, due to inadequate capture and recapture rates. Total annual mortality was 71%. The annual exploitation rate (54%) was greater than natural mortality rate (17%), however both fishing and natural mortality exhibited seasonal variation and peaked during the spring months, during peak fishing season, in 2012 and 2013. Competitive interactions appeared negligible in January 2013, with a Schoener's Index of 0.087, but a significant diet overlap, Schoener's Index of 0.85, was found in April 2013, especially between juvenile White Bass (<220 mm) and large White Perch (>160 mm). Stable isotope analysis also revealed that the niche size of White Perch expanded as they grew, resulting in the highest degree of overlap occurring between large White Perch and all size classes of White Bass. We found that White Bass did not use any specific habitat throughout the year, but concentrated in several high use areas of the reservoir. White Bass exhibited seasonal distribution patterns and were located off shore and in the deeper water in the winter or cooler months. White Bass had a relatively fast growth rate (K=0.67±0.13; median±SD) and had a truncated age distribution, dominated by individuals less than age 4. Sample size and other contributing factors resulted in a limited analysis of the White Perch telemetry data. Overall, the high estimated seasonal fishing mortality, truncated age distribution, and the increased diet overlap in the spring suggests that adjusting the current liberal harvest limits, especially in the spring, may help sustain reservoir White Bass populations.

Potential Mechanisms Underlying a Perceived White Bass *Morone chrysops* Decline in a Southeastern Reservoir

by
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BIOGRAPHY

I was born in Ann Arbor MI and grew up Canton MI, a once-small town filled with farm land and forests. It was in Canton where I spent many hours exploring the woods and ponds in our backyard. Summers spent camping on the Little Muskegon River in Michigan and growing up in a state with a lake culture are what sparked my interest in aquatic ecosystems.

I graduated from Salem High School in 2006 and moved on to Michigan State University to pursue a B.S. in Fisheries and Wildlife. Choosing a degree was easy for me, as I was blessed with a childhood filled with great outdoor experiences. I wanted a career where I could work toward keeping the beautiful lakes and their intricate ecosystems intact for future generations to experience. After graduation in 2010, I worked at the USGS Great Lakes Science Center as a student contractor on a river restoration project aimed to rebuild spawning populations of Lake Sturgeon and Lake Whitefish in the Detroit River. It was during my time at the Great Lake Science Center that I gained the confidence and experience needed to pursue a master's degree.

In 2011, I arrived at North Carolina State University to earn a master's degree in Fisheries and Wildlife Conservation Biology and to work with Drs. James A. Rice and D. Derek Aday on this project. My advisors and new friends have made this entire experience some of the best years of my life. The next stage in my life will hopefully be filled with the level of support and beauty I have experienced in North Carolina.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

POTENTIAL MECHANISMS UNDERLYING A PERCEIVED WHITE BASS *MORONE CHRYSOPS* DECLINE IN A SOUTHEASTERN RESERVOIR

INTRODUCTION

The White Bass *Morone chrysops*, native to the Mississippi River basin, is a popular sport fish in Midwestern and southern reservoirs. Reports indicate that White Bass are among the most commonly harvested species in Nebraska (Bauer 2002), Texas (Betsill and Pitman 2002), and South Dakota (Willis et al. 2002). White Bass exhibit high growth rates and are highly fecund, contributing to their success as a sport fish (Lee et al. 1980). Despite, or perhaps because of, their popularity, concern regarding declining White Bass populations began in the Great Lakes (Madenjian et al. 2000) when the abundance of age-0 White Bass sharply declined in the 1980s. Similar concerns expressed for some reservoir populations initiated an American Fisheries Society symposium (Guy et al. 2002a, and associated papers) that focused on White Bass ecology and management, and aimed to improve understanding and management of the species. Despite these efforts many reservoir populations may be declining and we still have a limited understanding of the underlying mechanisms. This project aimed to address some of the mechanisms that may be affecting White Bass populations.

One potential mechanism that could cause White Bass declines in reservoirs is mortality, especially fishing mortality. Typical harvest restrictions for White Bass are fairly liberal, which could lead to high exploitation rates. In North Carolina there is no closed season, a 25 daily fish harvest limit, and no length restriction; this management strategy is common in other states as well (Lovell and Maceina 2002). While White Bass have been documented as old as age 14 (Willis et al. 2002), populations in Missouri (Colvin 2002a), Alabama (Lovell and Maceina 2002), and Nebraska (Bauer 2002) have been shown to have truncated age distributions. Willis et al. (2002) found that few fish survived past age 5, especially in southern reservoirs. Annual mortality in one study increased from 40% in fish less than age 4 to 80% in fish older than age 4 (Colvin 2002a). Truncated age distributions suggest that these populations may already be experiencing the effects of high exploitation (Hsieh et al. 2010) and because of this may be vulnerable to more frequent fluctuations in abundance (Anderson 2008). Annual estimates of fishing mortality vary widely, ranging from 11-40% in five Kansas reservoirs (Shultz and Robinson 2002) and from 15-35% in Missouri reservoirs (Colvin 2002a). Natural mortality rates, estimated to be around 56% (Shultz and Robinson 2002), are rarely obtained because of the difficulty in physically observing natural deaths and separating natural from fishing mortality (Hightower et al. 2011). We also currently lack data on intra-annual variation in mortality for White Bass, which would be particularly valuable when attempting to quantify mortality for a species subject to a high degree of seasonality in fishing pressure (Lovell and Maceina 2002; Willis et al. 2002). White Bass experience increased angling pressure during spring spawning runs as they migrate from the lacustrine portion of the reservoir to inflowing streams and rivers where they often become highly concentrated (Muoneke 1994). It is not uncommon for harvest rates to peak during this period (Willis et al. 2002). Betsill and Pitman (2002) found that almost half of the angling effort in one Texas reservoir occurred in the inflowing river. Although creel surveys suggest seasonal changes in fishing pressure, it is essential to quantify monthly fishing and natural mortality when dealing with potentially declining populations.

A second potential mechanism underlying perceived White Bass population declines is trophic interactions between White Bass and invasive White Perch *Morone americana*. Native to the North Atlantic coast of the United States, White Perch are known for their ability to successfully invade systems and have expanded their range to the Great Lakes (Scott and Christie 1963; Busch et al. 1977; Boileau 1985) and reservoirs throughout North Carolina (Wong et al.1999), Oklahoma (Kuklinski 2007), Virginia (Harris 2006) and other southeastern and Midwestern states. The establishment of White Perch is associated with documented adverse effects on White Bass in the Great Lakes (Gopalan et al. 1998; Madenjian et al. 2000) and is suspected to be similarly affecting White Bass in reservoirs (Wong et al. 1999; Harris 2006; Feiner 2013a, 2013b), yet the underlying interactions are not well understood. In the Great Lakes, studies have suggested that egg predation by White Perch (Shaeffer and Margraf 1997) and a reduction in recruitment resulting from potential competition (Madenjian et al. 2000) may be contributing factors. In reservoirs there has been a focus on understanding potential competitive interactions between White Perch and White Bass that might influence resource use and niche overlap (Kuklinski 2007; Feiner et al. 2013a). Equivocal results of diet investigations have led to ambiguity over the level of overlap between White Bass and White Perch consumption patterns; recent investigations have indicated both moderate (Kuklinski 2007) and significant overlap (Feiner et al. 2013a). Stable isotope analysis (SIA), however, is a more integrated signal of trophic interactions and niche overlap between species and has provided evidence of significant trophic overlap between White Perch and, in particular, juvenile White Bass (Feiner et al. 2013a). Thus, although stomach content and stable isotope analyses indicate that competitive interactions may exist, questions still remain about the importance of these interactions and their potential to affect White Bass populations.

In addition to the uncertainty over competitive interactions and mortality rates, fishery biologists and managers currently lack a clear understanding of White Bass life history related to important parameters such as seasonal habitat use and distribution patterns. For example, while it is known that reservoir White Bass make a spring migration (Muoneke 1994; Willis et al. 2002; Betsill and Pittman 2002), little is known about their habitat use and distribution throughout the lacustrine portion of the system during non-spawning periods. Use of telemetry to follow seasonal distribution patterns would yield information about how White Bass use lake systems after spawning, and would allow us to contextualize intra-annual variation in mortality rates and identify where potential competitive interactions are occurring. Further, White Bass have often proven to be difficult to sample year round (Colvin 2002b). Identifying key habitats or distribution patterns throughout the year may aid in more effective sampling apart from the spawning run. We are aware of only one telemetry study that provides information on reservoir distribution throughout the year (Willis et al. 2002).

The goal of our investigation was to examine two potential drivers of White Bass population declines in reservoirs, fishing mortality and competitive interactions with White Perch, and to provide critical information regarding habitat use and seasonal movement patterns, particularly during non-spawning periods. The objectives of this study were to (1) estimate instantaneous monthly and annual fishing and natural mortality of White Bass, (2) compare diet and niche overlap between White Bass and White Perch through stomach content and stable isotope analysis, and (3) use telemetry to examine habitat use and movement patterns of reservoir White Bass throughout the year in Jordan Lake, a large, eutrophic southeastern reservoir.

METHODS

Study Site

B. Everett Jordan Reservoir (Jordan Lake) is a relatively shallow impoundment (mean depth of 5 m; Wong et al. 1999) located in the Piedmont region of North Carolina originally created for flood control (Figure 1.1). Jordan Lake is comprised of four main sub-basins that were assigned names for the purposes of this study; Farrington, Upper Jordan, Lower Jordan, and Haw, the latter including the Haw River arm of the reservoir and the mouth of the river itself (Figure 1.1). Jordan Lake is located near two densely populated cities, Durham and Raleigh, NC, and is a popular lake for recreational activities including sport fishing.

Since its impoundment in 1981 Jordan Lake has experienced dynamic changes in fish communities (Wong et al. 1999). Although non-native to the Piedmont region of North Carolina, White Bass have been present and managed in Jordan Lake since the first sampling efforts began in 1983 (C. Oakley, North Carolina Wildlife Resources Commission, personal communication). White Bass have been a popular sport fish in the system, especially during the spring migration into the Haw River. Jordan Lake also has a well established White Perch population. White Perch were first detected in Jordan Lake in 1988 and became abundant by 1994 (Wong et al. 1999). Since the invasion of White Perch, the North Carolina

Wildlife Resources Commission (NCWRC) has documented declines in catch rates of White Crappie *Pomoxis annularis*, Bluegill *Lepomis macrochirus*, and Flat Bullheads *Ameiurus platycephalus*, and expressed concerns about potentially declining White Bass (Wong et al. 1999).

Telemetry

We used telemetry to estimate mortality and address the spatial components of this study, movement and habitat use. White Bass were collected using boat electrofishing in spring 2012 and 2013 in the Haw River during the spawning run (Figure 1.1). Sampling was conducted by NCWRC and North Carolina State University personnel. We surgically implanted VEMCO (VEMCO, Ltd., Nova Scotia, Canada) V9-2L (29 x 7 mm; 4.7 g) acoustic coded transmitters into 50 White Bass weighing more than 235 g, generally greater than 270 mm, in March 2012 and 25 White Bass in April 2013. Transmitters were pre-programmed to include a passive and an active tracking period over a 30 day cycle; during the active tracking period transmitters emitted a signal every 15-45 s and for the remaining days the transmitters emitted a signal at a slower rate (110-390 s) or were off (Table 2.1). Following Murray (2002), fish were placed in a 64-L induction tank containing 100 mg/L Tricaine methanesulfonate (MS-222). Anesthetized fish were transferred to a surgery table and water containing a maintenance dose of 50 mg/L MS-222 was continuously pumped over the gills. Using a sterile scalpel an incision was made just below the pelvic fins and a transmitter was inserted into the intracoelomic cavity. Incisions were closed with 2-3 interrupted sutures using suture kits that included a 3-0 polydioxanone (PDS II) absorbable synthetic monofilament material and a FS-1 23 mm reverse cutting needle (Ethicon, Inc., Cornelia, GA). After surgery, fish recovered in a 64-L holding tank before being released. A 30 day pilot study found 100% tag retention in similarly-sized hybrid White Bass X Striped Bass *Morone saxatilis*, so we assumed zero tag loss in released White Bass.

We used a combination of passive and active approaches to relocate fish. From March 2012-October 2013 we relied on an array of continuously operating VEMCO VR2W receivers placed strategically throughout the lake to detect large scale movement of tagged fish (Figure 1.1). In the Haw River arm of the reservoir, about 1,500 m below the mouth, we set a gate consisting of two receivers placed approximately 500 m apart to detect upstream and downstream movement during the spawning run. To detect potential escapement from the reservoir, a receiver was placed 400 m downstream of the B. Everett Jordan Dam.

We conducted 19 monthly active tracking efforts from April 2012-October 2013. To ensure full coverage of the study system we established a series of listening points approximately 700 m apart throughout the lake (Figure 1.1). We listened for 90 s at each listening point, first with a VEMCO VR165 omnidirectional hydrophone and, when a fish was detected, a VR110 directional hydrophone to determine specific location. This approach provided a radius around each listening point of about 350 m (less than the detection range of our tags) and some degree of overlap in coverage (Figure 1.1). Using known locations of test tags placed in the water we determined our location accuracy to be within 2 m.

Mortality

To estimate instantaneous monthly fishing (F) and natural (M) mortality we first combined relocation data from our active and passive tracking efforts to create a capture history. A modified version of the multistate model in Chapter 9 of Kerry and Schaub 2011 was created in OpenBUGS v. 3.2.2 (© Free Software Foundation, Inc. 2007) using the capture history as the input. This model also built upon other previous models that used telemetry to estimate mortality (Hightower et al. 2001) and was created in conjunction with an additional telemetry mortality model that is under development (J. Hightower, unpublished data). This model consisted of a state process, including the true state of the fish in time *t* given the fish's state in time *t*-1, and an observational process, which was the probability of observing each fish's capture history in time *t* given the fish's state in time *t*. The observation matrix consisted of three probabilities in which a fish was either detected alive, detected and determined to have died from a natural mortality, or not detected. In the state matrix individual fish were determined to be alive, dead due to a natural mortality, or harvested. Monthly *F* and *M* were used to calculate monthly and annual total mortality (*A*), survival (*S*), exploitation (*u*), and natural mortality (*v*). Annual estimates were obtained by first averaging the monthly instantaneous rates for *F*, *M*, and *Z* estimated over 17 months, then scaling that average to a 12 month period.

Although we could not directly observe fish, any fish relocated in the same spot for three consecutive months was categorized as a natural mortality (Bendock and Alexandersdottr 1993). A fish no longer located in the system was assumed to have been harvested. Additional model assumptions were: (1) transmitter loss or failure was negligible, (2) there was no catch-and-release mortality, (3) undetected emigration did not occur, (4) no tagged fish were removed from the system via predation, (5) every fish had an equal probability of being detected each search period, (6) every fish had an equal chance of surviving from one search period to the next, and (7) all fish acted independently of each other. To ensure that mortalities were not due to surgery we omitted any passive relocation data less than two weeks after tagging.

White Bass Interactions with White Perch

To assess potential competition for resources, White Perch and White Bass were collected for stomach content and stable isotope analysis. Diet overlap was compared in January and April 2013. For the winter stomach content analysis, White Bass were collected in January 2013 by using overnight offshore gillnets set by the NCWRC throughout Lower Jordan and Haw (Figure 1.1). Two types of gill nets were used: the first was an experimental gill net that consisted of seven individual panels of 38-, 44-, 51-, 57-, 64-, 70-, 76-mm bar mesh sizes randomly distributed in 8.7 m sections across a single gill net. The other type was a single mesh gill net that consisted of uniform 38-, 51-, or 64-mm bar mesh size across each individual net. White Bass were sorted into small, medium, and large size bins (≤240 mm, 241-300 mm, and >300 mm) and placed on ice until our goal of 15 fish in each size category was met (our goal was not always met; Chapter 1 Results). White Perch used for stomach content analysis in January 2013 were collected by setting two 2 m x 38 m nearshore experimental mesh gillnets, consisting of five 7.6 m panels of 12.7, 19.1, 25.4, 38.1, and 50.8-mm bar mesh sizes and three 2 x 50 m nearshore gillnets consisting of 25.4-mm bar mesh in the lower basin of the lake, Lower Jordan. Nets soaked for 4-6 hours during the day. White Perch were also sorted into small, medium, and large size classes (≤120 mm, 121-160 mm, >160 mm) and collected until our goal of at least 15 fish in each size class was obtained. White Bass and White Perch were also collected for diet analysis in April 2013, via electrofishing near the mouth of the Haw River until at least 15 fish in each size class were collected. The first 15 White Bass collected from each size class during spring electrofishing were used for SIA in addition to diet analysis. To collect White Perch for SIA in April 2013 we followed the same sampling procedure as in January 2013. We aimed to collect White Perch from the lake to use for SIA because stable isotopes provide a temporally integrated measure of food consumption, and we assumed White Bass remained in the lake a majority of the year. Pelagic and littoral baseline samples for SIA were also collected in spring 2013. For the pelagic baseline, we collected zooplankton from several pelagic sites throughout Lower Jordan. Phytoplankton and predatory zooplankton were removed in the laboratory. We used a Ponar grab to take benthic samples near shore, typically in 0.5-1.0 m of water, to collect Chironomidae larvae for the benthic baseline.

In the laboratory, stomachs for stomach content analyses were removed and contents were emptied into vials containing 70% ethanol. Contents of White Perch and White Bass stomachs were sorted into individual categories of prey, including fish, Chironomids, other benthic invertebrates, zooplankton, various eggs, and other (which included detritus, rocks, and mussels). For each stomach individuals in each prey category were counted and weighed in aggregate to the nearest 0.01 g. Categories weighing less than 0.01 g were assigned a weight of 0.005 g.

To quantify diet overlap we first calculated percent frequency of occurrence (% FO), one of the more robust diet measurements relative to percent weight, percent volume, and percent number (Baker et al. 2014). We used Schoener's Index to calculate diet overlap as follows:

$$C_{\mathrm{xy}} = 1 - 0.5\ (\Sigma|P_{\mathrm{xi}} - P_{\mathrm{yi}}|)$$

where C_{xy} is the Schoener's Index between species or size class x and species or size class y, P_{xi} is the % FO of diet item i for species or size class x, and P_{yi} is the % FO of diet item i for species or size class y (Schoener 1970). Schoener's Index ranges from 0 (no overlap) to 1 (absolute overlap) and a value of 0.6 or higher was used as a threshold to indicate significant diet overlap (Wallace 1981).

Stable isotope analysis was done by removing a 12 x 12 mm cube of muscle tissue below the dorsal fin of each fish and sending it to the Cornell University Stable Isotope Lab, where ratios of heavy to light nitrogen isotopes ($\delta^{15}N$) and carbon isotopes ($\delta^{13}C$) were measured using a Finnigan MAT Delta Plus isotope ratio mass spectrometer (IRMS). Because nitrogen isotopes are typically assumed to have an enrichment factor of 3.4 ‰ with each increase of trophic level, $\delta^{15}N$ is often used to determine trophic level (Owens 1987). It was our intention to calculate trophic level following the equations developed in Post et al. (2002), however we were unable to do so due to inadequate baseline values that would have resulted in potentially inaccurate trophic level calculations. We ultimately used ANOVA in program R v 2.15.1 to test for differences in mean $\delta^{15}N$ and mean $\delta^{13}C$ among the size classes of White Bass and White Perch.

To compare isotopic niche overlap between White Bass and White Perch in all size classes we used Stable Isotope Bayesian Ellipses in R, or SIBER, a Bayesian model developed by Jackson et al. (2011) to calculate and plot the Bayesian standard ellipse area (SEAb), or the isotopic niche area of each species and size class. This model used $\delta^{13}C$, which provides information on whether food consumption is derived primarily from benthic or pelagic resources (Post 2002) and δ^{15}N of individual fish to calculate the SEAb, or isotopic niche area, for each size class for each species. Trophic niche overlap and the general trophic position of each size class for both species could then be compared by plotting the SEAb (δ^{13}C as the x-axis and δ^{15}N as the y-axis).

Movement and Habitat

Each time a fish was located during active tracking we recorded water depth, distance to shore, substrate type (predominately sand, silt, or gravel), and Global Positioning System (GPS) coordinates of the location. For the purposes of analysis monthly habitat and distribution data were aggregated by spring (April-June), summer (July-September), fall (October-December), and winter (January-March). We used Kolmogorov-Smirnov tests conducted in R to determine whether lake depth or distance to shore varied seasonally. Substrate was homogeneous across fish locations so no statistical analyses were conducted.

To characterize seasonal distributions of tagged White Bass we analyzed relocation data from passive and active tracking in Microsoft Excel 2007 (Microsoft® 2007) and ArcGIS Desktop 10 (© Copyright 2013 Esri). To do this, two separate files were created for every season. The first file converted individual fish locations from active tracking to a density parameter (fish per km^2) using the point density tool in ArcGIS 10. The second used the number of unique fish detected on each passive receiver per season, and scaled the size of the symbol representing each receiver relative to the number of fish detected. We then combined these two files to create seasonal maps depicting seasonal distribution and high use areas.

RESULTS

Telemetry

Tagged fish measured 309.9±23.8 mm (mean±SD) in 2012 and 356.5±18.3 mm in 2013 (Table 1.1). An equal number of males and females were tagged each spring (Table 1.1). There were no suspected surgery related deaths in 2012 and three surgery related deaths in 2013, which were censored from analysis. Receivers, continuously monitoring from March 2012-October 2013, recorded a combined total of 480,511 detections for 72 unique fish. Only one emigrating fish was detected on the receiver below the dam, and was subsequently censored from analysis. Monthly tracking efforts from April 2012-October 2013 resulted in a total of 371 fish relocations. By the end of the study (October 2013) only five fish remained with active tags in the system. Transmitters from 2012 were expected to expire late August 2013 and thus our mortality estimate only extended to August 2013.

Mortality

Our model estimated a median annual instantaneous fishing mortality rate (F) of 0.94 (95% credible interval: 0.49, 1.51) and an annual instantaneous natural mortality rate (M) of 0.20 (0.14, 0.57; Table 1.2). This translated into an annual total mortality (A) of 0.71 (0.60, 0.84), with an exploitation rate (u) of 0.54 (0.31, 0.71) and a natural mortality rate (v) of 0.17 (0.08, 0.36). Both F and M appeared to vary seasonally and peaked in April 2012 and in spring months (April, May and June) in 2013; overall, F appeared to be high compared to M during spring months. Consequently, survival was low during April 2012 and April, May, and June 2013.

White Bass Interactions with White Perch

For diet analysis, we collected 74 White Bass in January 2013, 65 (12 small, 14 medium, 39 large) with stomach contents and 45 White Perch, 35 (16 small, 15 medium, 4 large) with stomach contents. Of 48 White Bass collected in April 2013, 31 (8 small, 7 medium, 16 large) had food in their stomachs, and 30 (1 small, 15 medium, 14 large) of 49 White Perch contained stomach contents. Different patterns in diet composition among size classes occurred in January and April. In January 2013, minute diet overlap occurred between all size classes of White Bass and White Perch (Schoener's Index: 0.087; Table 1.3), as White Bass fed almost exclusively on fish and White Perch consumed mostly zooplankton, Chironomids and other benthic invertebrates (Figure 1.3a). More specifically, no significant overlap was found among size classes of White Bass and White Perch in January 2013 (Figure 1.3b; Table 1.3). However, in April 2013, White Bass increased their consumption of Chironomids and other benthic invertebrates and decreased fish consumption resulting in a greater and significant overlap with White Perch (Schoener's Index: 0.845), which mostly consumed Chironomids and benthic invertebrates (Figure 1.3a; Table 1.3). In particular, significant overlap occurred between large White Perch and all sizes of White Bass; however, because White Bass became more piscivorous with increasing size, the greatest overlap occurred between large White Perch and small White Bass (Schoener's Index: 0.96; Figure 1.3c; Table 1.3).

Our stable isotope analysis revealed minor differences in δ^{13}C and δ^{15}N between White Bass and White Perch. White Bass had significantly higher δ^{15}N values (ANOVA: F=3.92; df=99; P=0.003), however, pair-wise comparisons revealed that only large White

Bass had greater δ^{15}N values than small White Perch (Tukey's HSD: df=99; *P*=0.001; Table 1.4). The isotopic values for the pelagic (15.9, -23.4; δ^{15}N, δ^{13}C) and benthic (13.28, -25.0) baselines did not appear to be typical baseline values for the species we used or the system (Feiner et al. 2013a) and thus trophic level was not calculated. Mean δ^{13}C values varied significantly (ANOVA: *F*=11.55; df=99; *P*<0.001) between White Bass and White Perch, and particularly between small and medium White Perch and large White Bass (Tukey's HSD: $P \leq 0.01$; Table 1.4); no significant difference (Tukey's HSD: $P \geq 0.76$) was found between large White Perch and small, medium and large White Bass.

The Bayesian standard ellipse areas (SEAb) for each size class of both species revealed variation in trophic niches as size increased for both species. White Perch ellipse size increased directly with fish size; small to medium White Perch increased their δ^{15}N range (NR) and medium to large White Perch increased their δ^{13}C range (CR; Figure 1.4; Table 1.4). Conversely, White Bass ellipse area decreased with increasing fish size and all size classes remained similar in δ^{13}C and δ^{15}N ranges (Figure 1.4; Table 1.4). This resulted in a great deal of niche overlap between large White Perch and all size classes of White Bass. Due to small White bass having the largest SEAb of the White Bass size classes, the greatest overlap appeared to occur between large White Perch and small White Bass. There was no observable niche overlap between the small and medium White Perch and all size classes of White Bass (Figure 1.4).

Movement and Habitat Use

Data from our active tracking efforts revealed that White Bass did not concentrate in any particular habitat, such as sandy coves or near woody debris. Instead, White Bass were mostly pelagic throughout the year as 83% of fish relocations were at 50-300 m from shore. Distance to shore and depth at location were not correlated (r= 0.0039). Fish were located farther from shore in the winter (148±35 m; mean±SE) compared to spring 2012 (60±31 m) and spring 2013 (63±14 m; Kolmogorov–Smirnov test: $D \geq 0.365$; $P \leq 0.07$; Figure 1.5a). Fish were also located in deeper water in the winter than all other seasons (Kolmogorov–Smirnov test: $D \geq 0.35$; $P < 0.01$; Figure 1.5b). White Bass concentrated in several large areas of the lake and their movement between these high-use areas as well as between sub-basins of the lake varied seasonally and annually (Figure 1.6). High-use areas were mostly located throughout the deepest sub-basins, the Haw River arm and Lower Jordan (Figure 1.6). While fish tended to move between sub-basins from one high use area to another, generally using the lower, deeper basins the most (Figure 1.6a), some variation in lake use occurred between years and cohorts of tagged fish. For example, in 2012, 30% of tagged fish immediately dispersed to Upper Jordan and Farrington within two weeks and 60% were detected using these uppermost basins throughout the remainder of spring 2012 (April-June). In contrast, in spring 2013 both newly tagged White Bass and surviving fish tagged in 2012 did not disperse as quickly or as much as newly tagged fish in 2012. Only 12% of fish tagged in 2012 used the uppermost basins during April-June 2013. None of the fish tagged in 2013 moved into the uppermost basins within two weeks after tagging and only 16% of them were detected in the upper basins throughout spring 2013.

DISCUSSION

Our results indicate that fishing mortality and interactions with White Perch may both contribute to perceived declines in reservoir White Bass populations. Our estimated annual fishing mortality (54%) was greater than all previous estimates we are aware of, which range from 15-35% in Missouri reservoirs (Colvin 2002a) and 11-40% in Kansas reservoirs (Shultz and Robinson 2002). Conversely, the annual natural mortality was lower (17%) in our study than in Kansas reservoirs (56%; Shultz and Robinson 2002). The general lack of published natural mortality estimates precludes making broader comparisons; however, our results indicate that fishing mortality may be affecting White Bass populations more than natural mortality. Heavy exploitation has been shown to lead to increased fluctuations in abundance (Anderson et al. 2008). Heavily truncated age distributions, such as the distribution we observed in Jordan Lake where no fish older than age 4 were found, are often a result of high exploitation rates. This appears to be a common occurrence in reservoir White Bass populations, especially in southern systems (Colvin 2002; Lovell and Maceina 2002; Chapter 2). White bass recruitment often is highly erratic (Colvin 2002a; Ahrens et al. 2010) and can vary with factors such as prey base (Shultz et al. 2002) and reservoir inflow (DiCenzo and Duval 2002; Shultz et al. 2002), resulting in variable year-class strength. High mortality due to fishing pressure over successive years combined with highly variable recruitment could, therefore, be affecting the abundance of White Bass in Jordan Lake and other reservoir populations.

One option to reduce fishing mortality is increasing harvest restrictions by reducing bag limits or implementing size limits. Currently, little is known about the effectiveness of enforcing minimum length limits on reservoir White Bass populations as few states impose length limits for White Bass (Lovell and Maceina 2002; Muoneke 1994). Some studies suggest a minimum length limit may help recover faster growing and heavily exploited populations that also experience low natural mortality, such as the population in Jordan Lake (Guy et al. 2002b; Lovell and Maceina 2002). Given the significant fishing mortality estimated in this study, reducing the bag limit (currently 25 fish a day in North Carolina) may also be an effective option. This might cause an in increase in catch-and release mortality (indistinguishable from natural mortality in our model), however, there may still be an overall increase in the number of mature individuals remaining in the system, especially during the spawning run when fishing mortality peaks. Before adjusting harvest restrictions, creel surveys to quantify metrics such as the catch-and-release rate, the number of White Bass kept each fishing period, the timing of peak fishing pressure during the spawning run, overall fishing pressure, size of harvested fish, and the types of bait used may be useful to determine how effective additional restrictions will be.

While our model shows clear seasonal patterns in fishing and natural mortality, it also has several limitations. First, our assumption of no catch-and-release mortality may have been violated. Anecdotal observations indicated that some anglers did release White Bass, so catch-and-release mortality could potentially be contributing to the high natural mortality rates we estimated during the spring when fishing pressure increases. Currently there are no estimates, to our knowledge, of catch-and-release mortality for reservoir White Bass populations. Combining telemetry tags with tag return data from traditional tags has been used to estimate catch-and-release mortality and may be a useful adaptation to our model (Bacheler et al. 2009). Our model also could not distinguish between predation (e.g., predatory birds) that may have removed fish from the system and angler harvest. As acoustic telemetry tags have a negligible detection range out of water, this is a common limitation of models applied to aquatic acoustic telemetry models. One remedy could be to use radio telemetry tags, which have a better terrestrial range, to determine bird or mammal predation and compare estimates to our results. Ultimately, failure to separate bird and mammal predation from harvest would result in an inflated *F* whereas failure to separate indirect fishing mortality, due to catch and release, from natural mortality would result in a deflated *F*. It seems unlikely in our study that removal of tagged fish via predation would have been common enough to inflate our estimates of *F* given the large size of tagged fish and their tendency to remain offshore and in deep water. Catch-and-release mortality during the spring spawning run could have resulted in the underestimation of *F;* given that our estimate is already relatively high, however, that possibility would not change the interpretation of our data. .

Our study revealed that spring is a crucial time for reservoir White Bass populations and their management, as both fishing and natural mortality and diet overlap with White Perch increased during spring months. Creel surveys have provided evidence that fishing pressure on White Bass increases in the spring; Betsill and Pitman (2002) found that half of the angling time recorded in a Texas reservoir occurred during the spring, and in Missouri River reservoirs in South Dakota harvest also peaked in May and June (Willis et al. 2002). However, as far as we are aware, our study is the first to estimate monthly instantaneous rates of fishing and natural mortality for White Bass. Further, this is the first study to quantify the temporal pattern of White Bass natural mortality, which also peaked during spring. This suggests that reinforcing mechanisms may be driving declines in White Bass populations: high fishing pressure results in high fishing mortality, which occurs during an energetically costly period when fish may be experiencing higher than normal rates of natural mortality (Guy et al. 2002b). Although some apparent natural mortality may actually be due to catch-and-release mortality, a spike in natural mortality after spawning may be expected due to the associated energetic costs. Finally, as diet overlap with White Perch increased substantially during the spring, potential competition may be adding stress during this time if resources are limited. Restrictive harvest limits and additional enforcement might be options to mitigate the increased mortality experienced by White Bass during their spawning run.

Stable isotope and diet analysis revealed further evidence that juvenile White Bass and large White Perch share similar resources through trophic niche and diet overlap. Our investigation shows that White Perch expand their niche size as they increase in size, first along the nitrogen spectrum and then along the carbon spectrum. As a result, large White Perch have the largest niche area, which completely encompasses all sizes of White Bass. In other North Carolina reservoirs, medium White Perch had the largest niche area (Feiner et al. 2013a). White Bass exhibit the opposite pattern, decreasing niche size and becoming more specialized with increasing fish size and, consequently, juvenile White Bass encounter the greatest degree of niche overlap with large White Perch. The high diet overlap we observed in spring between large (i.e., >160 mm) White Perch and small (i.e., <240 mm) White Bass is consistent with the results from our stable isotope analyses and with previous investigations that have indicated moderate to significant overlap between White Perch and juvenile White Bass less than 200 mm TL (Kuklinski 2007; Feiner et al. 2013a). In addition to conducting a comprehensive diet analysis that evaluates overlap during all seasons, it may also be useful to learn whether resource availability, specifically for juvenile White Bass, varies seasonally throughout the lake and the river. Evidence from this study and previous studies (Kuklinski 2007; Feiner et al. 2013a) is consistent and suggests that overlap between adult White Perch and juvenile White Bass poses the greatest potential for competition (other than possible overlap during earlier life history stages that hasn't been evaluated). Given limited resources, that could be a contributing factor in declining White Bass populations in reservoirs where White Perch are established (Feiner et al. 2013a).

Stable isotope analysis can be powerful tool for fishery scientists to better understand trophic interactions and intricate food webs in aquatic ecosystems, however, quality baseline samples are necessary to obtain reliable trophic level estimates. This proved difficult in our study as our baseline samples did not appear to accurately represent their assumed baseline trophic position. In particular, the isotopic values for the benthic baseline (Chironomids), assumed to be $\delta^{13}C$ enriched from consuming plant material and algae in the littoral zone (Peterson and Fry 1987), were actually more $\delta^{13}C$ depleted than the pelagic baseline. Chironomids have been shown to exhibit high intraspecific variability among individuals from the same lake depending on life stage and where samples were collected (Grey et al. 2004). It is possible the individuals we collected were more $\delta^{13}C$ depleted than other individuals and were thus not representative of the true baseline. In addition, both the benthic and pelagic baselines were $\delta^{15}N$ enriched, and only slightly below the $\delta^{15}N$ values of our fish. Finally, the $\delta^{15}N$ values for White Bass (17.9, 18.6; min, max) and White Perch (17.2, 18.2) from our system appeared to be greater than the $\delta^{15}N$ of White Bass (12.5, 14.9) and White Perch (10.8, 11.9) in Lake James, another North Carolina reservoir, but similar to the $\delta^{15}N$ range found for White Perch in Jordan Lake in a previous study (Feiner et al. 2013a, 2013b), suggesting that Jordan Lake may be more nitrogen enriched than other systems. Even though we could not estimate trophic levels in this study, the relative comparison of δ^{15}N and δ^{13}C values among species and size groups is valid, which allowed us to confidently interpret the pattern of niche overlap between large White Perch and all size classes of White Bass.

The movement and distribution patterns we observed for White Bass did not suggest any localized habitats, such as sandy coves or areas with woody debris, where competitive interactions with White Perch might be significant, but it did provide insight as to how White Bass use reservoirs outside of their predictable spawning run. Difficulty in locating White Bass for efficient sampling outside the spawning season is a common problem in managing White Bass populations (Colvin 2002b). Our study provided evidence of predictable patterns, similar to those found by Willis et al. (2002), showing that White Bass concentrated relatively far offshore and in deep waters during the winter. These patterns, in addition to the high-use areas we identified, may aid in increasing the efficiency and effectiveness of sampling White Bass, allowing managers to potentially obtain more frequent and reliable population parameters important for the management of a potentially declining species.

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TABLES

Table 1.1: Mean length (SD) and weight (SD) of fish implanted with acoustic V9-2L transmitters in 2012 and 2013.

	N	Length	Weight
		2012	
Total	50	309.9 (23.8)	384.7 (96.7)
Females	25	318.4 (25.6)	436.2 (97.2)
Males	25	302.0 (20.4)	337.2 (68.4)
		2013	
Total	25	356.5 (18.3)	677.7 (117.9)
Females	12	363.3 (20.6)	740.3 (119.2)
Males	13	350.2 (13.8)	620.0 (85.2)

Table 1.2: Annual and monthly fishing (*F*), natural (*M*), and total (*Z*) instantaneous mortality rates, total mortality (*A*), survival (*S*), exploitation rate (*u*) and natural mortality (*v*) for White Bass in Jordan Lake in 2012 and 2013.

	F	M	Z	A	S	u	v
Annual	0.94	0.2	1.23	0.71	0.29	0.54	0.17
	(0.49, 1.51)	(0.14, 0.57)	(0.91, 1.82)	(0.60, 0.84)	(0.16, 0.40)	(0.31, 0.71)	(0.08, 0.36)
				2012			
Apr	0.19	0.01	0.21	0.19	0.81	0.17	0.01
	(0.03, 0.39)	(0.00, 0.08)	(0.05, 0.40)	(0.04, 0.33)	(0.67, 0.96)	(0.03, 0.32)	(0.00, 0.07)
May	0.05	0.00	0.06	0.06	0.94	0.05	0.00
	(0.00, 0.20)	(0.00, 0.04)	(0.00, 0.21)	(0.00, 0.19)	(0.81, 1.00)	(0.00, 0.18)	(0.00, 0.04)
Jun	0.05	0.00	0.05	0.05	0.95	0.05	0.00
	(0.00,0.19)	(0.00, 0.04)	(0.00, 0.20)	(0.00, 0.18)	(0.82, 1.00)	(0.00, 0.17)	(0.00, 0.04)
Jul	0.02	0.00	0.02	0.02	0.98	0.02	0.00
	(0.00, 0.14)	(0.00, 0.05)	(0.00, 0.15)	(0.00, 0.14)	(0.86, 1.00)	(0.00, 0.13)	(0.00, 0.04)
Aug	0.02	0.00	0.02	0.02	0.98	0.02	0.00
	(0.00, 0.13)	(0.00, 0.05)	(0.00, 0.15)	(0.00, 0.14)	(0.86, 1.00)	(0.00, 0.13)	(0.00, 0.05)
Sep	0.02	0.00	0.03	0.03	0.98	0.02	0.00
	(0.00, 0.15)	(0.00, 0.05)	(0.00, 0.16)	(0.00, 0.14)	(0.86, 1.00)	(0.00, 0.14)	(0.00, 0.05)
Oct	0.00	0.00	0.01	0.01	0.99	0.00	0.00
	(0.00, 0.05)	(0.00, 0.05)	(0.00, 0.08)	(0.00, 0.07)	(0.93, 1.00)	(0.00, 0.05)	(0.00, 0.05)
Nov	0.00	0.00	0.00	0.00	1.00	0.00	0.00
	(0.00, 0.04)	(0.00, 0.05)	(0.00, 0.07)	(0.00, 0.07)	(0.93, 1.00)	(0.00, 0.04)	(0.00, 0.05)
Dec	0.00	0.00	0.00	0.00	1.00	0.00	0.00
	(0.00, 0.04)	(0.00, 0.05)	(0.00, 0.07)	(0.00, 0.07)	(0.93, 1.00)	(0.00, 0.04)	(0.00, 0.05)

Table 1.2 Continued

	F	M	Z	A	S	u	v
				2013			
Jan	0.00	0.00	0.00	0.00	1.00	0.00	0.00
	(0.00, 0.04)	(0.00, 0.05)	(0.00, 0.07)	(0.00, 0.07)	(0.93, 1.00)	(0.00, 0.04)	(0.00, 0.05)
Feb	0.00	0.00	0.00	0.00	1.00	0.00	0.00
	(0.00, 0.04)	(0.00, 0.05)	(0.00, 0.07)	(0.00, 0.07)	(0.93, 1.00)	(0.00, 0.04)	(0.00, 0.05)
Mar	0.07	0.00	0.08	0.07	0.93	0.07	0.00
	(0.00, 0.28)	(0.00, 0.05)	(0.00, 0.29)	(0.00, 0.25)	(0.75, 1.00)	(0.00, 0.25)	(0.00, 0.05)
Apr	0.39	0.16	0.56	0.43	0.57	0.30	0.12
	(0.11, 0.67)	(0.05, 0.39)	(0.29, 0.61)	(0.25, 0.59)	(0.42, 0.75)	(0.09, 0.46)	(0.04, 0.28)
May	0.12	0.11	0.26	0.23	0.77	0.11	0.10
	(0.00, 0.44)	(0.02, 0.36)	(0.05, 0.61)	(0.05, 0.46)	(0.54, 0.95)	(0.00, 0.34)	(0.02, 0.29)
Jun	0.35	0.00	0.36	0.30	0.70	0.29	0.00
	(0.11, 0.79)	(0.00, 0.08)	(0.11, 0.81)	(0.11, 0.55)	(0.44, 0.89)	(0.10, 0.55)	(0.00, 0.07)
Jul	0.02	0.00	0.03	0.03	0.97	0.02	0.00
	(0.00, 0.28)	(0.00, 0.11)	(0.00, 0.31)	(0.00, 0.26)	(0.74, 1.00)	(0.00, 0.24)	(0.00, 0.10)
Aug	0.03	0.00	0.05	0.04	0.96	0.03	0.00
	(0.00, 0.40)	(0.00, 0.10)	(0.00, 0.42)	(0.00, 0.34)	(0.66, 1.00)	(0.00, 0.33)	(0.00, 0.09)

Table 1.3: Schoener's Index values of diet overlap between all sizes of White Bass combined (Total White Bass) and all sizes of White Perch combined (Total White Perch) in January and April 2013 as well as between small, medium, and large size classes of both species. A sample size too small for analysis is indicated by *; significant overlap indicated in bold.

		Total White Bass	Small White Bass	Medium White Bass	Large White Bass
January	Total White Perch	0.087			
	Small White Perch		0.000	0.000	0.000
	Medium White Perch		0.038	0.038	0.088
	Large White Perch		*	*	*
April	Total White Perch	**0.845**			
	Small White Perch		*	*	*
	Medium White Perch		0.499	0.499	0.221
	Large White Perch		**0.962**	**0.876**	**0.607**

Table 1.4: Results from 2013 stable isotope analysis by species and size class, including sample size (*N*), the Bayesian standard ellipse (SEAb)(lower, upper quartile), mean δ^{13}C (SE), δ^{13}C range (CR), mean δ^{15}N (SE), and the δ^{15}N range (NR).

		N	SEAb	δ^{13}C	CR	δ^{15}N	NR
White Bass	Total	52		-25.9 (0.10)	5.5	18.1 (0.08)	6.4
	Small	19	2.13 (1.8, 2.5)	-25.6 (0.25)	5.5	17.9 (0.15)	3.0
	Medium	14	0.80 (0.7, 0.95)	-25.8 (0.07)	0.8	18.0 (0.10)	1.3
	Large	19	0.75 (0.64, 0.87)	-26.1 (0.06)	1.3	18.6 (0.10)	2.0
White Perch	Total	48		-27.7 (0.35)	11.6	17.9 (0.15)	5.8
	Small	8	1.28 (1.03, 1.62)	-28.6 (0.08)	1.0	17.2 (0.08)	1.2
	Medium	20	3.32 (2.87, 3.87)	-28.3 (0.43)	9.7	17.9 (0.28)	5.8
	Large	20	8.09 (6.99, 9.40)	-26.6 (1.07)	11.6	18.2 (0.29)	2.9

FIGURES

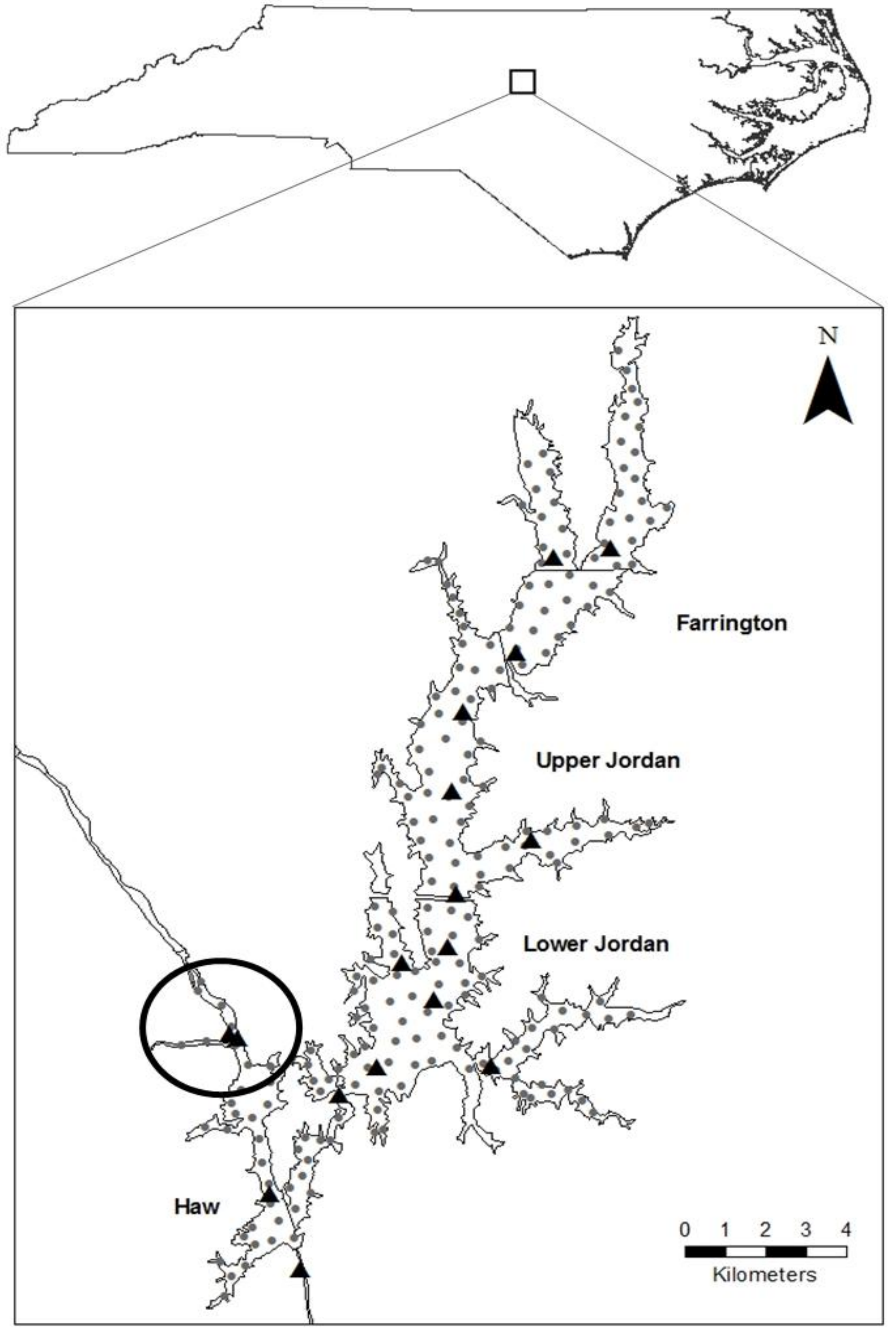

Figure 1.1: Map of Jordan Lake showing its location in central North Carolina, the tagging site in the mouth of the Haw River (black circle), sub-basins of the reservoir (labeled and delineated by gray lines), and locations of VR2W receivers (black triangles) and listening points (gray dots) used for passive and active tracking.

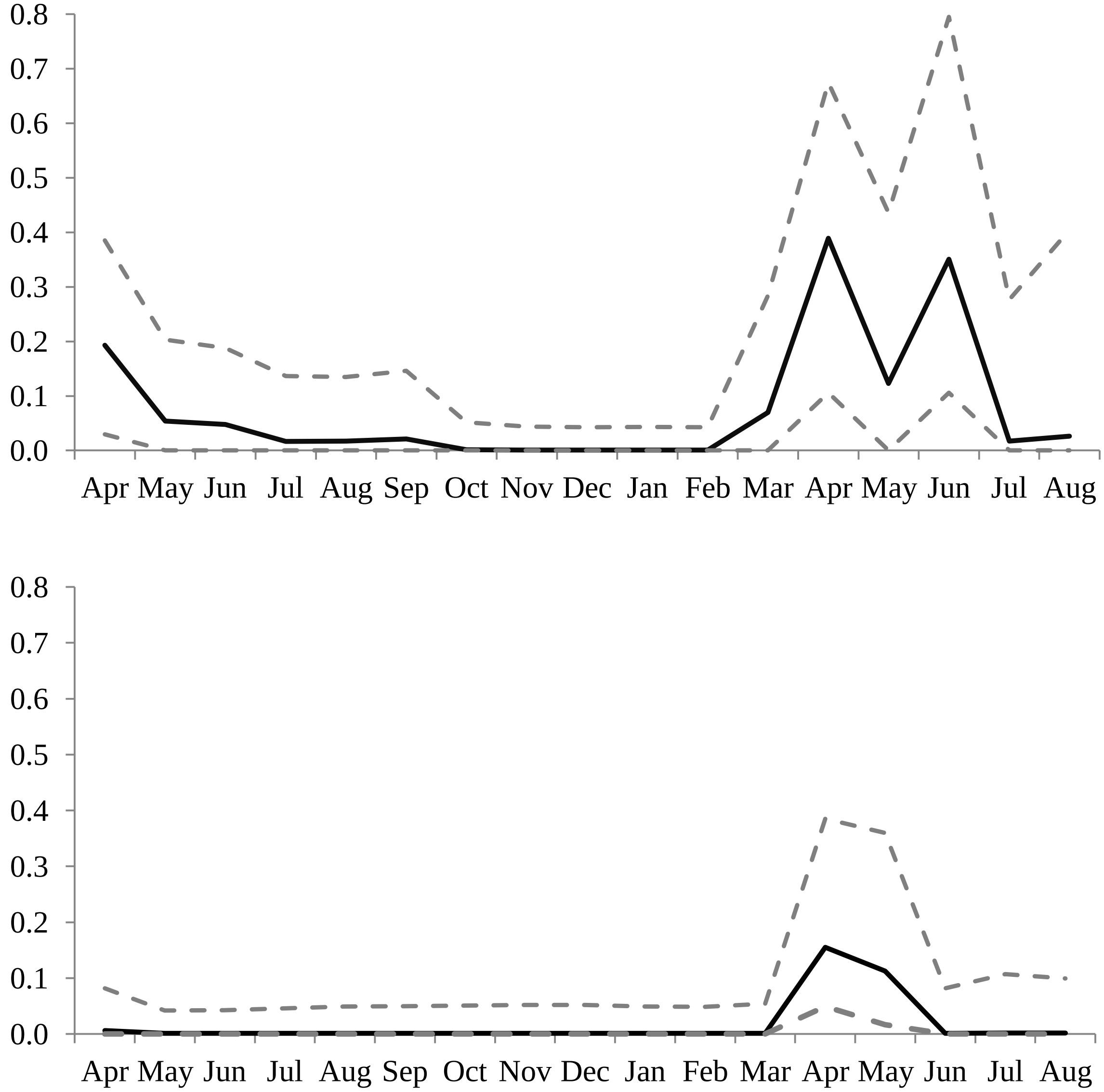

Figure 1.2: Instantaneous monthly fishing (*F*, upper panel) and natural (*M*, lower panel) mortality rates (solid lines) of White Bass in Jordan Lake from April 2012-August 2013. Dashed lines indicate 0.975th and 0.025th credible intervals.

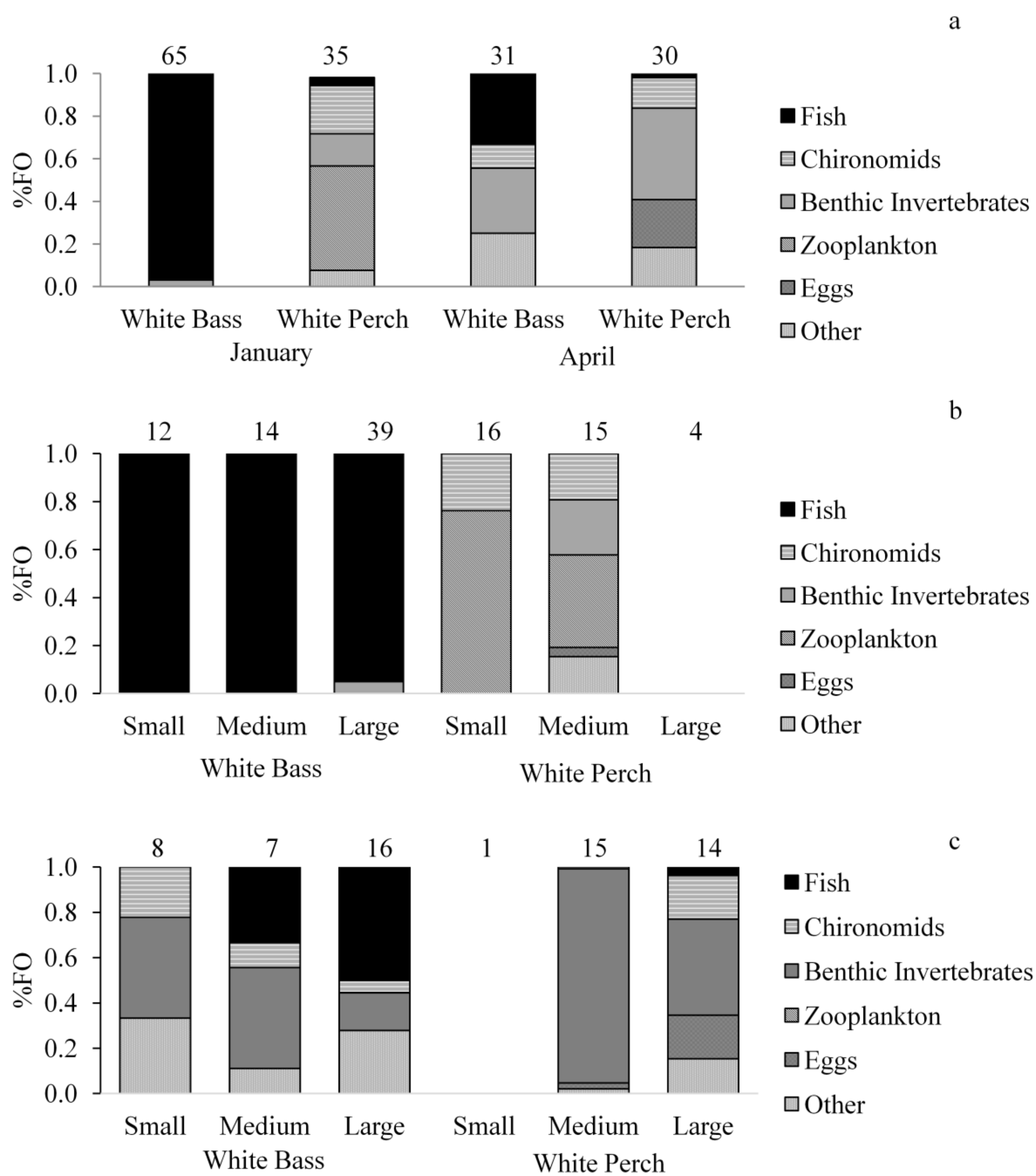

Figure 1.3: Diet composition of White Bass and White Perch collected in January 2013 and April 2013 for (a) all sizes combined, (b) small, medium, and large fish of both species in January 2013, and (c) small, medium, and large fish of both species in April 2013. Size groups with sample sizes too small for analysis were excluded.

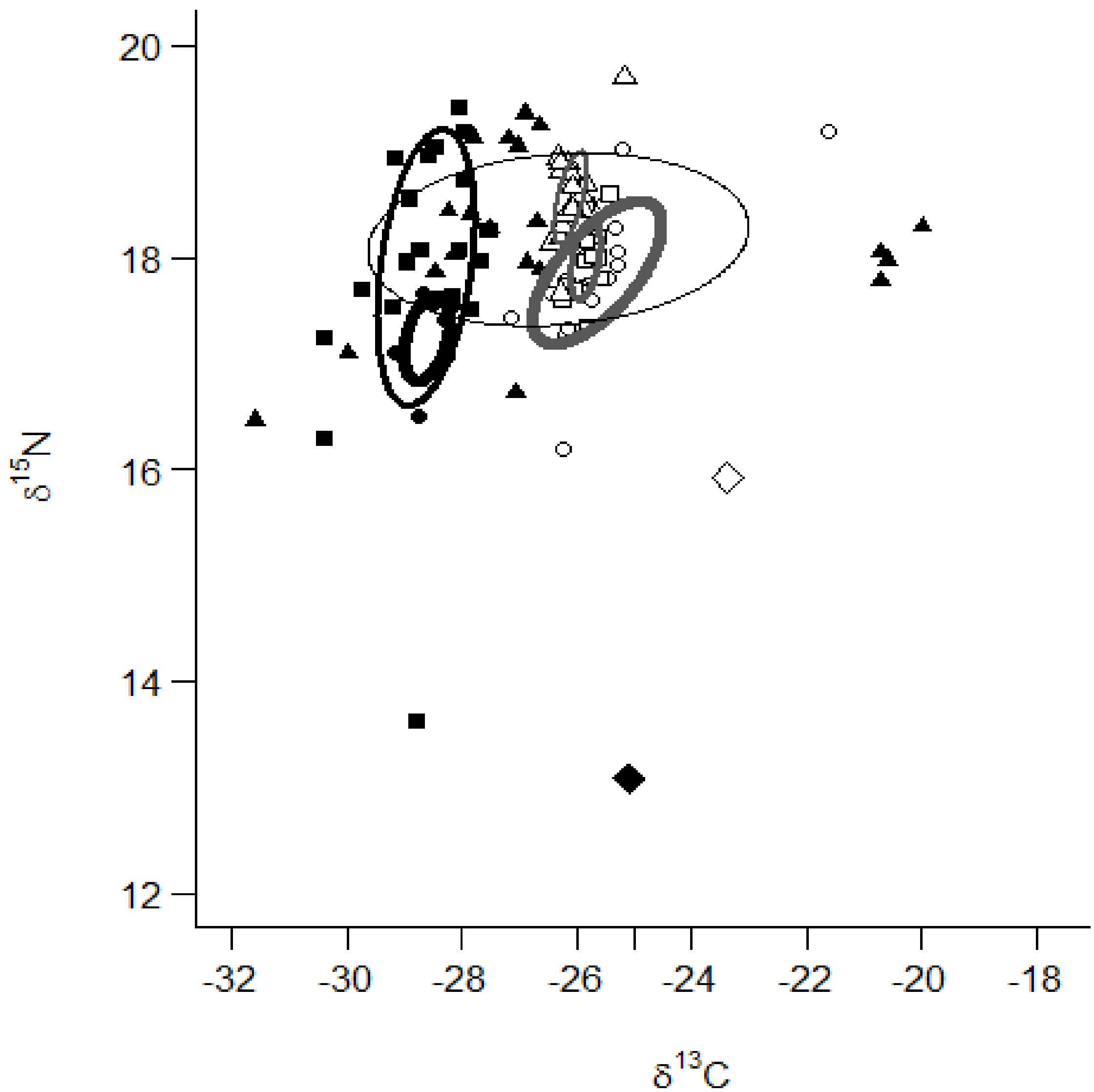

Figure 1.4: Bayesian standard ellipse area (SEAb) for small (thickest gray ellipse), medium (medium thickness gray ellipse), and large (thinnest gray ellipse) White Bass and small (thickest black ellipse), medium (medium thickness black ellipse), and large (thinnest black ellipse) White Perch. Isotopic values for individual fish for small (white circles), medium (white squares) and large (white triangles) White Bass as well as small (black circles), medium (black squares) and large (black triangles) White Perch, the pelagic baseline (large white diamond) and the benthic baseline (large black triangle) are shown.

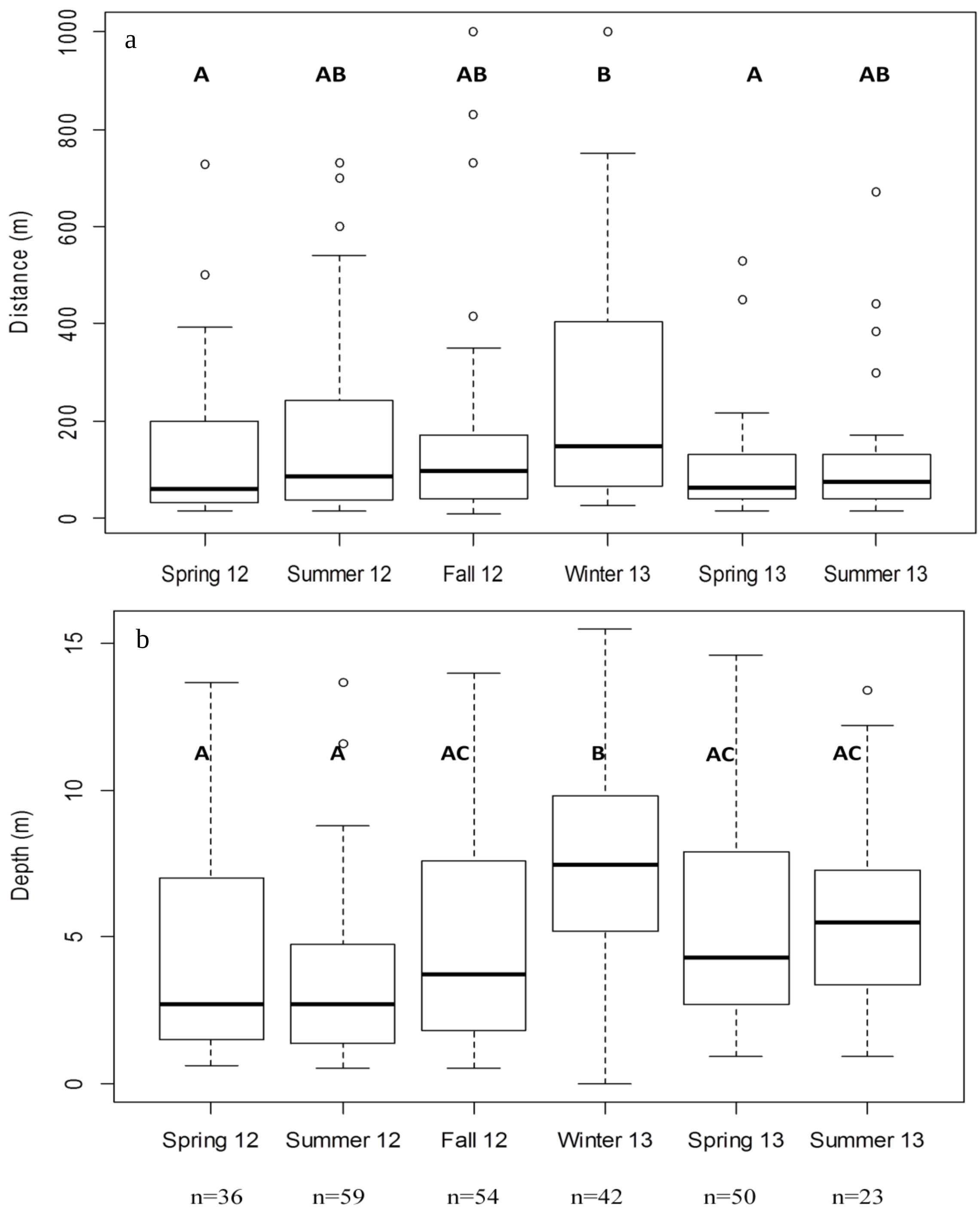

Figure 1.5: Seasonal variation, from spring 2012 through summer 2013, in (a) distance to shore and (b) depth where fish were relocated; heavy lines indicate medians, boxes indicate upper and lower quartiles, bars indicate maximum and minimum values, and circles indicate outliers; n is the number of observations.

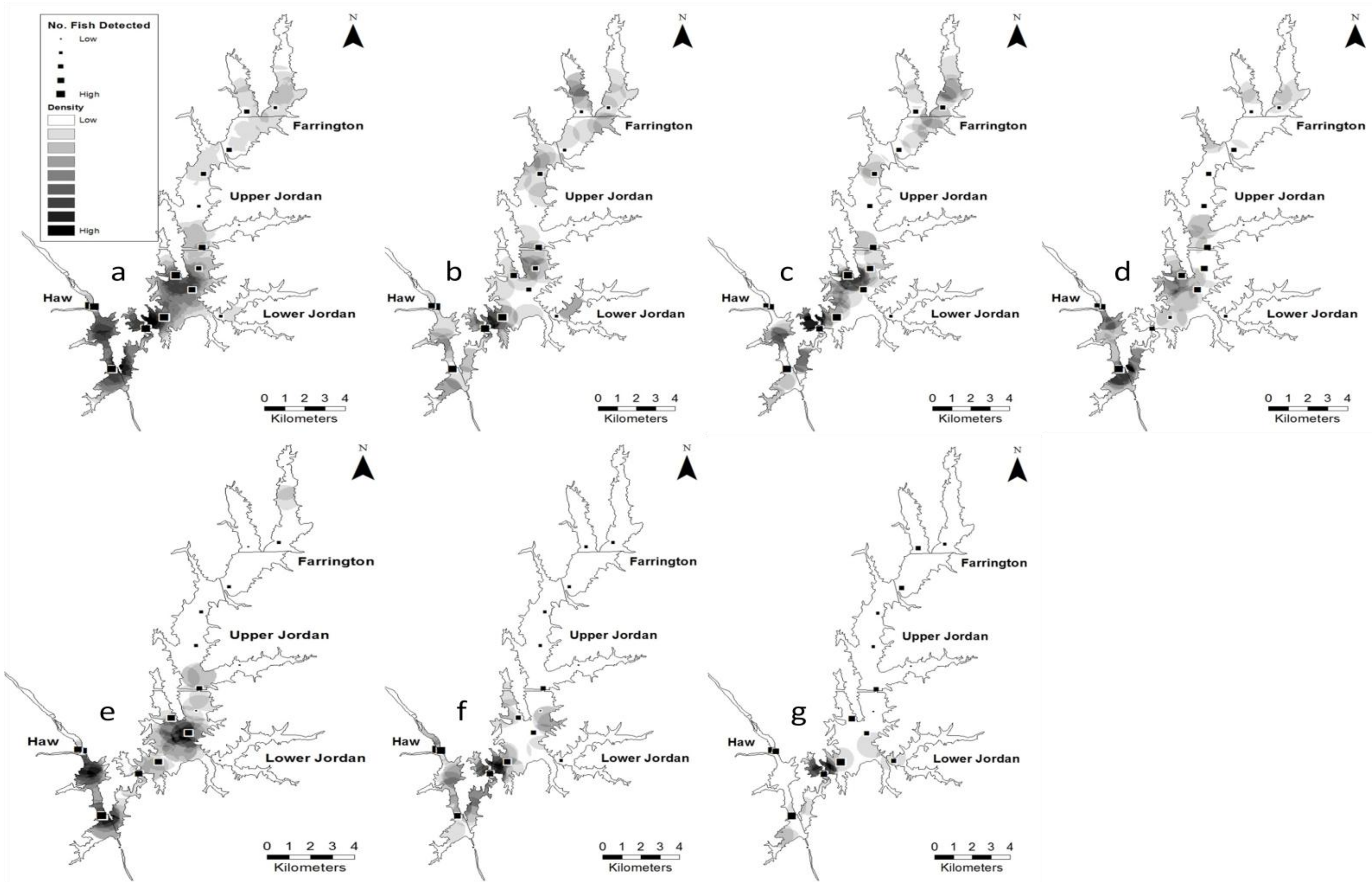

Figure 1.6: White Bass distributions during (a) the whole study, (b) spring 2012, (c) summer 2012, (d) fall 2012, (e) winter 2012-2013, (f) spring 2013, and (g) summer 2014. Density of White Bass (fish km^2), estimated from active tracking data is shown as the background gray scale. Black squares indicate passive receivers; size of the symbol increases with the number of unique fish detected per receiver.

ESTIMATION OF WHITE BASS POPULATION PARAMETERS AND POTENTIAL HABITAT OVERLAP WITH WHITE PERCH IN JORDAN LAKE, NC

INTRODUCTION

Although the White Bass *Morone chrysops* is a popular sport fish in many southeastern and Midwestern reservoirs, relatively little is known about its life history and ecology in lentic systems (Guy et al. 2002a). In addition, there have been concerns that White Bass are declining in some reservoirs, but the mechanisms associated with these declines are not well understood, making management of this species especially difficult. Several mechanisms contributing to population declines have been suggested, including high fishing mortality (Muoneke 1994; Chapter 1) and competitive interactions with invasive White Perch *Morone americana* (Gopalan et al. 1998; Madenjian 2000; Kuklinski 2007; Feiner 2013a, 2013b; Chapter 1). However, it remains difficult to make management decisions based on these potential mechanisms because our overall understanding of White Bass population dynamics is limited.

Information on population size, growth rates, and age structure can substantially enhance our ability to assess potential declines and associated mechanisms in White Bass populations. An estimate of population size can provide a valuable indication of status as well as provide a baseline from which to monitor fluctuations or trends. However, collecting a representative sample large enough to estimate population size (typically via mark-recapture methods) is particularly challenging for White Bass, as they are difficult to sample during most of the year (Colvin 2002b). Sampling during the spring spawning run provides the best opportunity to collect large numbers of fish, but collections are typically limited to spawning adults (Colvin 2002b). Growth rates and age structure of White Bass are also important as both parameters can influence population fluctuations and recruitment. White bass growth rates are known to vary widely among systems (Colvin 2002a), between sexes (Guy et al. 2002b), and by prey base (Bauer 2002). Data on age structure can provide information on the proportion of mature adults in the population and whether or not the population is dominated by strong year-classes. Although White Bass can live up to 14 years (Willis et al. 2002), many reservoir White Bass populations exhibit highly truncated age distributions, with few fish surviving past age 5 (Bauer 2002; Colvin 2002a; Lovell and Maceina 2002; Willis et al. 2002; Chapter 1). Colvin (2002a) found that annual mortality rates increased from 40% to 80% after age 4. Fluctuations in population abundance and truncated size and age distributions have historically been linked to high fishing mortality from over-exploitation (Anderson 2008). Thus, obtaining basic information on White Bass population characteristics is an important first step in understanding population dynamics and possible declines.

Coupled with a lack of basic information on White Bass is the absence of studies that examine whether direct competitive interactions between White Bass and White Perch are contributing to White Bass declines through similar habitat use or distribution patterns. While several studies have used stomach content and stable isotope analysis to explore potential resource overlap (Madenjian et al. 2000; Kuklinski 2007; Feiner et al. 2013a; Chapter 1), none, to our knowledge, compare potential spatial interactions between White Bass and White Perch. Individual habitat and distribution studies exist for White Bass (Willis et al. 2002; Martin et al. 2009) and White Perch (McGrath 2005; Divver 2012), but none directly evaluate the extent of overlap in habitat use or distribution patterns of these two species in systems where they co-occur. Despite being a common invasive species most movement studies of White Perch occur in their native range (McGrath 2005; Divver 2012). White Bass are typically thought to have large home ranges (Martin et al. 2009), whereas White Perch exhibit relatively small home ranges (McGrath 2005). White Bass are typically thought of as an open water pelagic species, whereas White Perch are a more littoral species using habitats with flat bottoms and sandy or soft substrates (Stanley and Danie 1983). In reservoirs, White Bass exhibit diel movement patterns and spring migrations related to spawning (Willis et al. 2002; Divver 2012). Though White Perch in their native range migrate to spawn in rivers, tributaries, or estuaries, very little is known about the seasonal distribution of White Perch in invaded systems. Thus, understanding whether White Bass and White Perch exhibit similar seasonal distribution patterns or occupy similar habitats may provide additional insight to where and when competitive interactions may be occurring.

The goal of this study was to quantify several key White Bass population parameters while also evaluating habitat and distribution similarities with White Perch in a southeastern reservoir where managers are concerned about a potential White Bass population decline. Our main objectives were to (1) estimate White Bass spawning population size using a mark-recapture approach, (2) determine White Bass growth and age structure, and (3) assess potential overlap in White Bass and White Perch distribution and habitat use using telemetry.

METHODS

Study Site

This study used the same study site, B. Everett Jordan Reservoir (Jordan Lake), and study design as a larger ongoing study investigating White Bass spatial distribution and mechanisms that could be causing their decline (Chapter 1). Jordan Lake was impounded in 1981 and White Perch wee first detected in 1988 (Wong et al. 1999). Thus, Jordan Lake is an excellent reservoir for comparing White Perch and White Bass habitat use and distribution patterns in a system as both species are well established.

Population Parameters

To estimate population size, we conducted a mark-recapture study from 2011-2013. Our approach was to use a modified mark-recapture model in which a sub-sample of the population is marked and re-marked over multiple occasions to estimate population size (N), apparent survival (φ), the number of new individuals entering the system (β), and the probability of detection (p) (Williams et al. 2002). White Bass were collected via electrofishing near the mouth of the Haw River by North Carolina Wildlife Resources Commission (NCWRC) and North Carolina State University personnel during the spring spawning run in March and April of 2011-2013. In 2011, each fish was weighed to the nearest 0.1 g, measured to the nearest mm total length (TL), and then a 12 x 2.15 mm Passive Integrated Transponder (PIT) tag, purchased from Oregon RFID (Copyright © 2014 Oregon RFID), was injected into its body cavity posterior to the pelvic fin. In 2012 and 2013, fish were scanned for an existing PIT tag to identify recaptures. In 2012, non-recaptured fish were weighed, measured, and injected with a PIT tag as in 2011.

We collected White Bass for age analysis during winter gillnetting and spring electrofishing in 2013. White Bass and White Perch that were brought back to the lab for stable isotope analysis and stomach content analysis (Chapter 1) in January 2013 and April 2013 were also used for age analysis. Both winter and spring fish samples were kept on ice and brought back to the laboratory where sagittal otoliths were removed. Otoliths were cleaned with water and soap, embedded in epoxy, sectioned transversely using a Buehler IsoMet® Low Speed Saw, mounted on a slide, and aged using a Nikon SMZ1000 microscope with a polarized lens. Otoliths were aged by two independent readers. Disagreements between the first two readers (which only happened twice), were resolved by an independent third reader. To estimate growth we fit mean length at age using the von Bertalanffy growth curve in OpenBUGS v. 3.2.2 (© Free Software Foundation, Inc. 2007) with the following equation:

$$l_t = L_\infty\left(1 - e^{-K(t-t_0)}\right)$$

where l_t is the estimated length at age t, L_∞ is the asymptotic length at which growth reaches zero, K is the estimated growth rate, and t_o is the estimated age at which l_t equals zero (Ricker 1975). We also examined the White Bass length frequency distribution by combining the length data from White Bass collected during all sampling efforts in 2011-2013.

Distribution and Habitat

We used acoustic telemetry to compare the distribution and habitat use of White Bass and White Perch. Data for White Bass were obtained from 75 fish implanted with acoustic VEMCO (VEMCO, Ltd., Nova Scotia, Canada) V9-2L (29 x 7 mm; 4.7 g) transmitters in

April 2012 (*N*=50) and March 2013 (*N*=25) as part of a more extensive study (Chapter 1). Data for White Perch were obtained from 20 fish implanted with VEMCO V7-4L (22.5 x 7 mm; 1.8 g) in October 2012, when White Perch reached a taggable size. White Perch weighing greater than 50 g, typically greater than 160 mm, were collected in the evening using boat electrofishing at three sites (identified as areas where White Bass concentrated during that particular time in our study) throughout Jordan Lake and the Haw River arm (Figure 2.1; Chapter 1). We followed the same surgery protocol and guidelines used for transmitter implantation in White Bass (Chapter 1). Both transmitter types were programmed to include passive and manual tracking periods when transmitters emitted a signal at slower or faster rates for intervals during a 30 day cycle (Table 2.1).

Tagged fish were relocated using a combination of passive and active tracking. Using an array of 17 passive continuous VEMCO VR2W receivers, fish were monitored from October 2012-May 2013. We conducted a range test with a test tag and an omnidirectional hydrophone and estimated the detection range for the receivers to be approximately 200 m for V7-4L transmitters and approximately 400 m for V9-2L transmitters (assuming the hydrophone and passive receivers had a similar range). Even with the larger detection range, coverage of the study area using only passive receivers would have been incomplete given the number of receivers available. Thus, receivers were distributed to detect large scale movement between sub-basins of Jordan Lake and included one receiver downstream of B. Everett Jordan Dam to detect any potential escapement from the system (Figure 2.1). Receivers were downloaded and maintained monthly. Monthly efforts were also made to locate tagged White Bass and White Perch. Transmitter programs were designed to have coinciding active tracking periods for both species, when transmitters emitted a signal every 15-45 s. The White Perch transmitters were designed to extend battery life and due to a smaller battery had a shorter tracking period (3 days) than the transmitters used in White Bass (5-12 days). To ensure the entire lake was searched, we created a series of listening points placed approximately 600-700 m apart for White Bass and 400-500 m apart for White Perch. At each point, we listened using a VEMCO VH165 omnidirectional hydrophone; if a fish was detected we then used a VEMCO VH110 directional hydrophone to locate the fish. At each fish location, we recorded the depth of the water column (m), distance to shore (m), substrate type (predominately sand, silt, or gravel), and the exact location using a Global Positioning System (GPS). To analyze the distribution data we combined active and passive tracking data of White Bass and White Perch from October 2012-May 2013. Using the program ArcGIS Desktop 10 (© Copyright 2013 ESRI), we created a series of files using the same protocol as in Chapter 1 to map their seasonal distribution. We tested for differences in the distributions of distance to shore and depth at location between species using a Kolmogorov-Smirnov test in R v 2.15.1 (© Free Software Foundation, Inc. 2007).

RESULTS

Population Parameters

For the population estimate we tagged 259 White Bass with PIT tags over three sampling trips in April 2011 (*N*=132 males; *N*=20 females; *N*=107 unknown; Table 2.2). In March and April 2012 we PIT tagged 133 fish over nine sampling trips, (*N*=89 males; *N*=32 females; *N*=12 unknown; Table 2.2) and recaptured 2 fish from 2011. In 2013, we scanned 82 fish for PIT tags and recaptured 1 fish from 2011 and 4 fish from 2012. Statistical consulting in 2013 revealed that a reliable population estimate was not feasible based on our collections to date, thus, no additional fish were PIT tagged in 2013 (apart from fish implanted with acoustic transmitters that also received PIT tags). Our low recapture rate (<1.0%) indicated that a much higher number of tagged fish would have been needed to obtain the precision required for an accurate estimate.

We aged 125 White Bass collected in 2013. Of these, 74 fish were obtained during January gillnetting and 51 were obtained from April electrofishing. In both cases fish from all size classes were collected. White Bass exhibited rapid growth (K=0.67±0.13; median±SD), reaching approximately 290 mm TL by age 2 with an asymptotic length of nearly 400 mm (L_∞= 396.6±19.7 mm; t_o =-0.31±0.19; Figure 2.2). The White Bass population in Jordan Lake was dominated by young fish (≤age 2) and exhibited a heavily truncated age distribution with ages ranging from 1-4 (Figure 2.3). In 2011 there appeared to be one year class dominating the size distribution consisting of fish ranging in size from 220-280 mm (likely age 1). This year class also dominated the size distribution in 2012 at age 2, ranging from 280-340 mm, and again at age 3 ranging from 340-380 mm in 2013 (Figure 2.4). In 2012 and 2013, the age-1 year class was not as pronounced as the 2011 age-1 year class. No young of the year White Bass were collected.

Distribution and Habitat

As a result of our manual tracking efforts a total of 23 White Perch relocations and 131 White Bass relocations from October 2012-May 2013 were used in our movement and habitat analysis. Tagged White Perch measured 163±5.3 mm (mean±SD) and weighed 51.4±5.6 g, resulting in tag weight that was on average 3.5% of fish body weight. Upon release, two White Perch were never detected and six were suspected mortalities by November. Thus, only White Perch that survived and were detected past November were used in our analysis (*N*=12). Distribution patterns between the two species during this time period varied slightly (Figure 2.5), however, due to the low number of White Perch relocations and because our comparisons for White Perch are based on 12 individuals, these results are inconclusive. Mainly, White Perch remained in the same sub-basin they were tagged in and did not move between sub-basins, whereas White Bass tended to move between sub-basins and exhibited seasonal movement patterns (Chapter 1). For example, 79% of White Perch were detected using only one sub-basin, whereas only 21% of White Bass were detected using one sub-basin October 2012-May 2013. Neither species appeared to concentrate in any particular habitat, but White Bass were located slightly closer to shore than White Perch (Kolmogorov–Smirnov test: *D*=0.392; *P*=0.028; Figure 2.6a). As an example, 87% of White Perch relocations were at 50-300 m from shore, whereas only 54% of White Bass relocations were at 50-300 m from shore. In addition, White Perch were never located less than 50 m from shore. White Bass and White Perch were located at similar lake depths of around 5 m (Figure 2.6b).

DISCUSSION

Our results revealed a White Bass population with a heavily truncated age distribution, reinforcing this common and potentially troubling theme in reservoir White Bass ecology (Colvin 2002a; Lovell and Maceina 2002; Willis et al. 2002). Similar to other studies, the White Bass population in our system appeared to be dominated by younger individuals (i.e., <age 4). Colvin (2002a) found most fish in four Missouri reservoirs were

less than age 4 and rarely found fish greater than age 7. Similarly, Lovell and Maceina (2002) found 98% of fish sampled in four Alabama reservoirs were younger than age 5. This truncated age distribution may be indicative of over exploitation. High fishing mortality due to over exploitation may be causing an increase in population abundance fluctuations (Anderson 2008). Frequent fluctuations in abundance, especially after consecutive years of low abundance, may lead managers to believe populations are declining. Truncated age distributions and population fluctuations may be sustainable, but are heavily reliant on the production of strong year-classes every 3-4 years (Lovell and Maceina 2002). While we observed one strong year class throughout this study, White Bass experience highly erratic recruitment (Shultz et al. 2002; Ahrens et al. 2010) resulting in erratic year-class strength (DiCenzo and Duval 2002). Failure to produce a strong year class every 3-4 years could potentially devastate a White Bass population.

The fast growth rate of White Bass found in this study was consistent with other studies. White Bass growth in Jordan Lake (K=0.67) appeared to fall within the growth rate range (K=0.50-0.89) found in four large Missouri reservoirs (Colvin 2002a). The asymptotic length found in this study (L_∞= 396.6 mm) also appeared to fall within a normal range found in other reservoirs. For example, Colvin (2002) found that White Bass asymptotic length varied from 396-449 mm. High growth rates allow many White Bass populations to reach their asymptotic length by age 3-4 (Lovell and Maceina 2002). However, according to our results, White Bass in Jordan Lake may not reach their asymptotic length until after age 4.

One potential solution to help to mitigate some of the fishing effects on White Bass populations would be to impose stricter harvest limitations. In the past it has been difficult to assess whether a minimum length limit is a successful management strategy for White Bass, as few states have enforced this practice (Muoneke 1994). Muoneke et al. (1994) found moderate benefits after instating minimum length limits in a previously unregulated Texas reservoir; generally speaking, the average fish size increased and more anglers practiced catch-and-release. Simulations of White Bass population dynamics in four Alabama reservoirs suggested that populations experiencing fast growth and high fishing mortality as well as a natural mortality rate of less than 30% may benefit from enforcing minimum length limits (Lovell and Maceina 2002). White Bass in Jordan Lake exhibited a relatively high growth rate, an especially high fishing mortality rate and a low natural mortality rate (Chapter 1), suggesting that minimum length limits could be useful in reducing impacts of fishing on this White Bass population.

Sampling White Bass remains difficult and, although White Bass are relatively abundant and accessible during their spring spawning run, it was not feasible, despite substantial effort, to obtain a large enough sample size to meet the capture and recapture rates needed to calculate a reliable population size estimate. Pollock et al. (1990) recommended a minimum Coefficient of Variation (CV) of 20% for Jolly-Seber mark-recapture models. The capture probability required to obtain a CV of 20% decreases with increasing number of sampling periods, apparent survival, and population size. Low survival, especially during the spring spawning run, and difficulty sampling White Bass throughout the year mean it is highly unlikely that we could achieve the substantially greater recapture probability needed to obtain a CV of 20%, even with much greater sampling effort. In addition, because of timing and the sampling methods used, young of the year White Bass were not targeted or caught, so had we been able to make an estimate it would have only applied to age-1 and older fish. As White Bass are difficult to sample year-round, obtaining accurate population estimates for the species has become a common problem (Colvin 2002b). A more feasible option for managers may be to focus on relative population abundance through other sampling methods such as fall gillnetting, suggested by Colvin (2002b) to be the least sex- or age-biased method to use.

Our ability to compare White Bass and White Perch movement and habitat use was hindered due to limited White Perch relocations. Difficulty collecting White Perch large enough to tag resulted in a tag weight averaging 3.5% of fish body weight. Consequently, this may have resulted in a high number of surgery-related mortalities. The White Perch transmitters also had a weaker power output and had about half the range of the transmitters used for White Bass. Our ability to relocate White Perch was further limited because the battery life of the smaller tags only allowed for three days of active tracking (compared to five days for White Bass). In the future, a more complete and rigorous comparison between White Bass and White Perch using telemetry would require a larger number of tagged White Perch, preferably of a size that would allow for a larger transmitter to be used.

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TABLES

Table 2.1: Transmitter schedules for White Bass tagged in March 2012 and April 2013 (V9-2L) and for White Perch tagged in October 2012 (V7-4L). The duration of each time step is given in days. The random delay time interval, when a transmitter emits a signal, is shown by number of seconds in parentheses for each step.

	2012 V9-2L	2013 V9-2L	2013 V7-4L
Step 1	5 (330-390)	12 (15-45)	15 (240-300)
Step 2	15 (110-250)	18 (110-250)	3 (15-45)
Step 3	5 (15-45)	12 (15-45)	12 (Off)
Step 4	5 (Off)	18 (110-250)	NA

Table 2.2: Number of fish PIT tagged and number of additional fish scanned for tags in years 2011-2013, mean length (SD), and mean weight (SD) of White Bass sampled for the mark-recapture study in the mouth of the Haw River during the spring spawning run in April 2011, and March and April 2012. Note fish tagged with acoustic tags in 2013 were also implanted with PIT tags.

Year	N Fish Tagged	N Fish Scanned	Total Length (mm)	Weight (g)	Recaptures from year: 2011	2012
2011	259		272.6 (32.8)	265.8 (101.6)		
2012	133	34	289.7 (37.2)	320.3 (114.0)	2	
2013	25	57	299.4 (58.3)	451.1 (234.5)	1	4

FIGURES

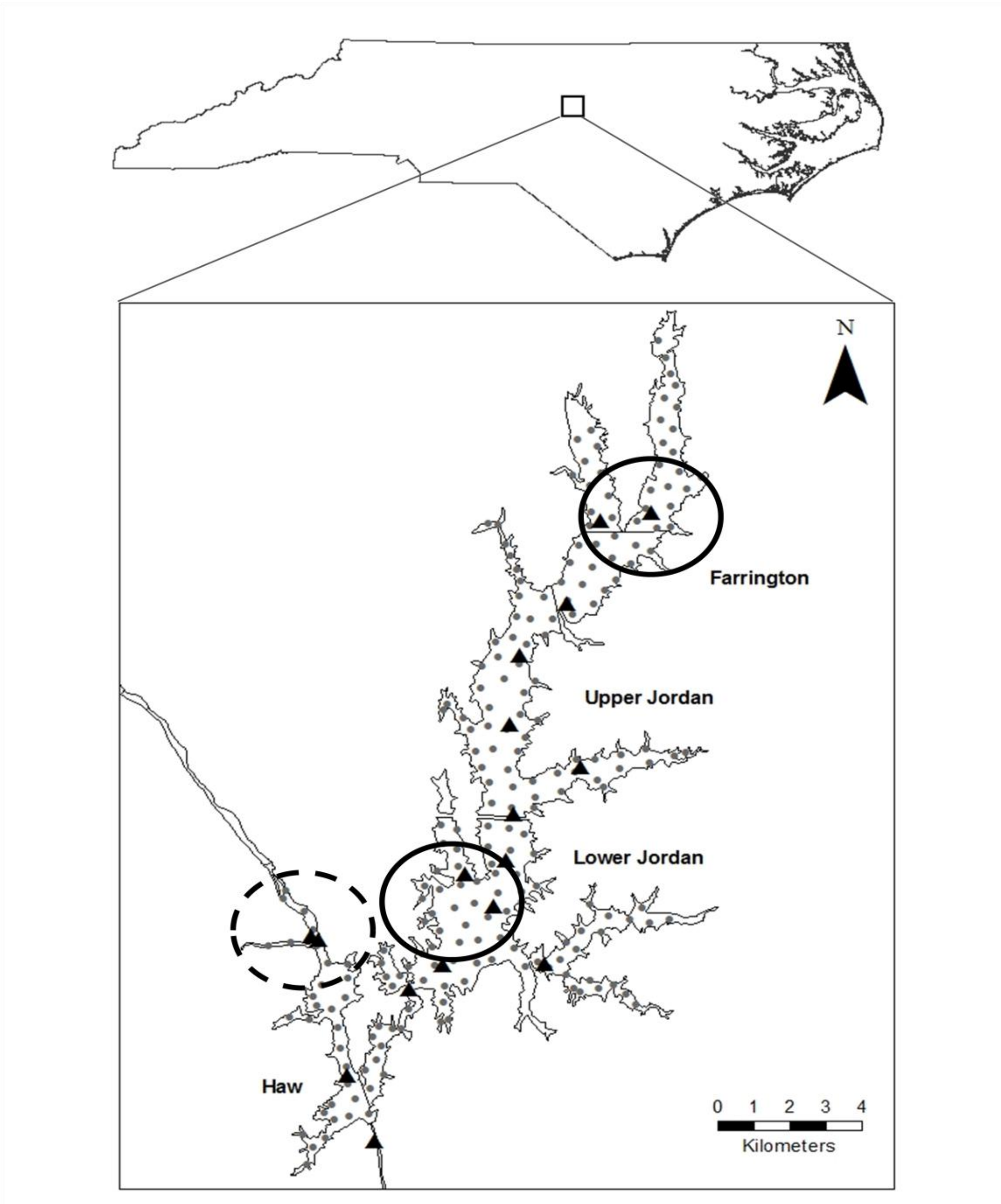

Figure 2.1: White Perch tagging sites in October 2012 (black circles) and combined White Bass tagging site in March 2012 and April 2013 and White Perch tagging site in October 2012 (dashed black circle). Receiver locations (black triangles) and White Bass listening points (solid gray circles) are also shown.

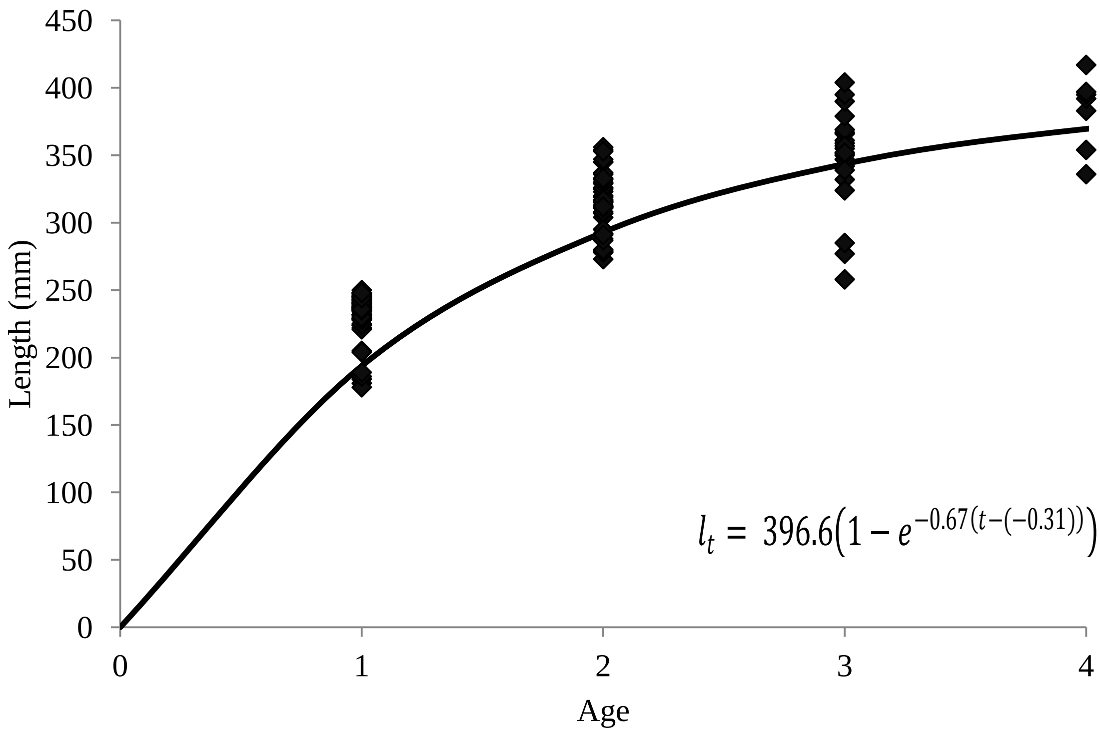

Figure 2.2: The von Bertalanffy Growth curve for White Bass collected via gillnet sampling throughout Lower Jordan and the Haw River arm in January 2013 and via electrofishing in mouth of the Haw River in April 2013.

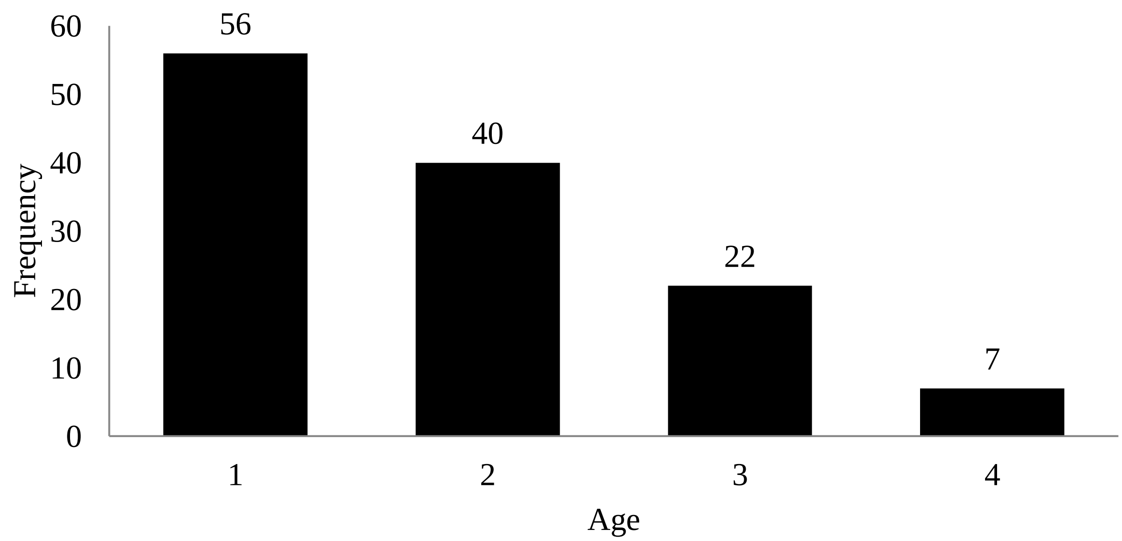

Figure 2.3: Age distribution of White Bass collected via gillnet sampling throughout Lower Jordan and the Haw River arm in January 2013 and electrofishing in the mouth of the Haw River in April 2013. Sample sizes are indicated above each bar.

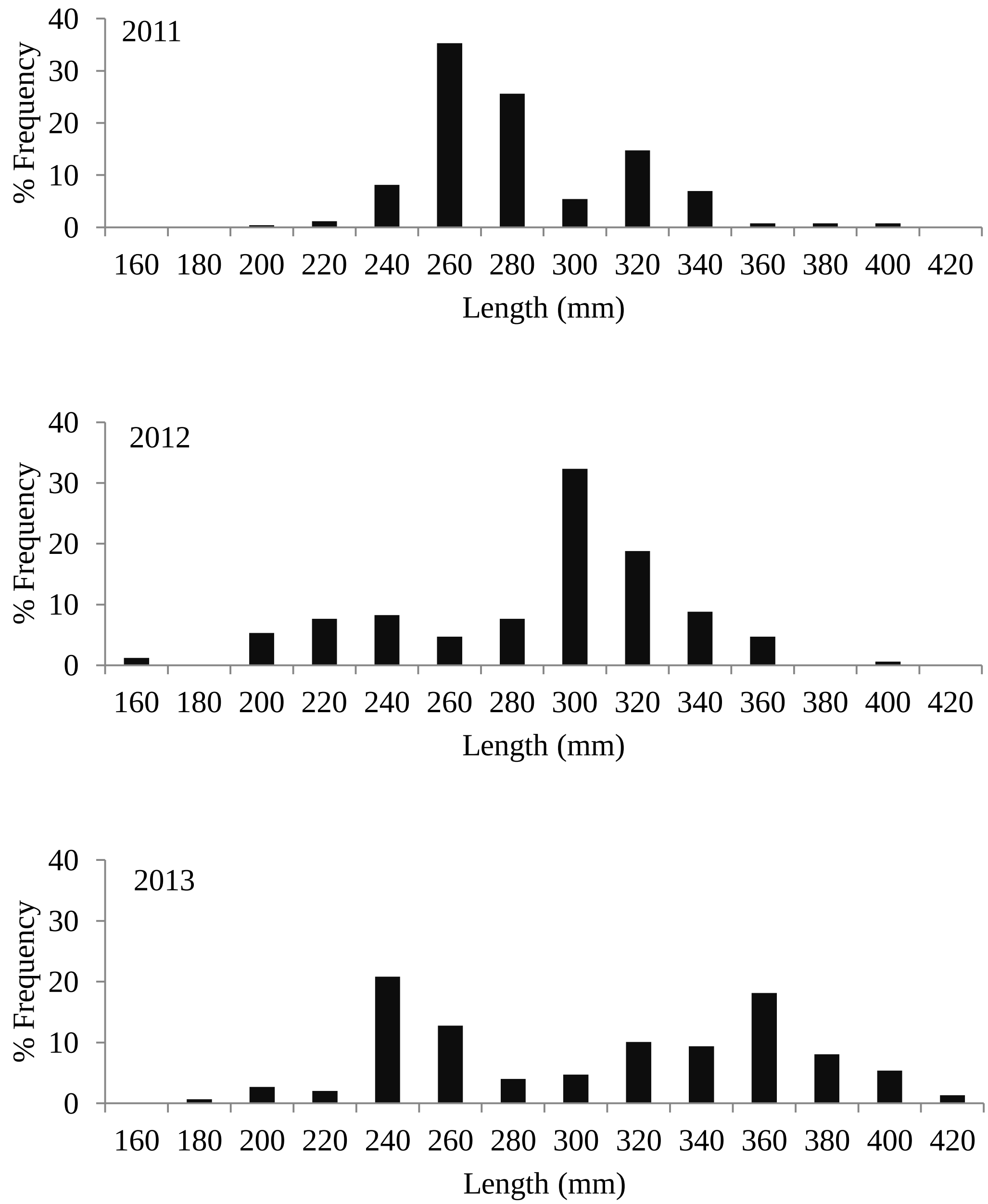

Figure 2.4: Length frequencies of White Bass collected by electrofishing in the mouth of the Haw River in April 2011, March and April 2012, and April 2013, and by gillnetting throughout Lower Jordan and the Haw River arm in January 2013.

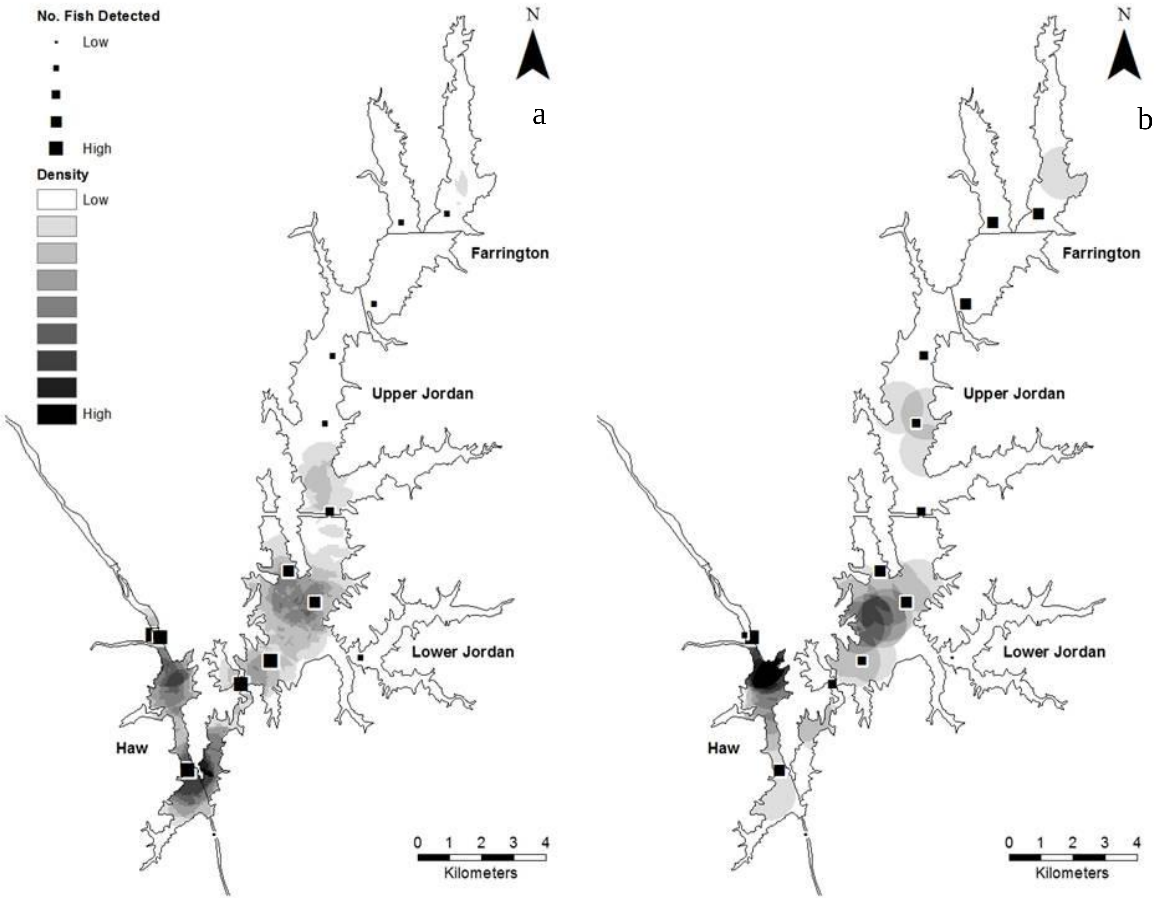

Figure 2.5: The distributions of (a) White Bass and (b) White Perch from October 2012-May 2013. Density of fish (fish km^2), estimated from active tracking data is shown as the background gray scale. Black squares indicate passive receivers; size of the symbol increases with the number of unique fish detected per receiver.

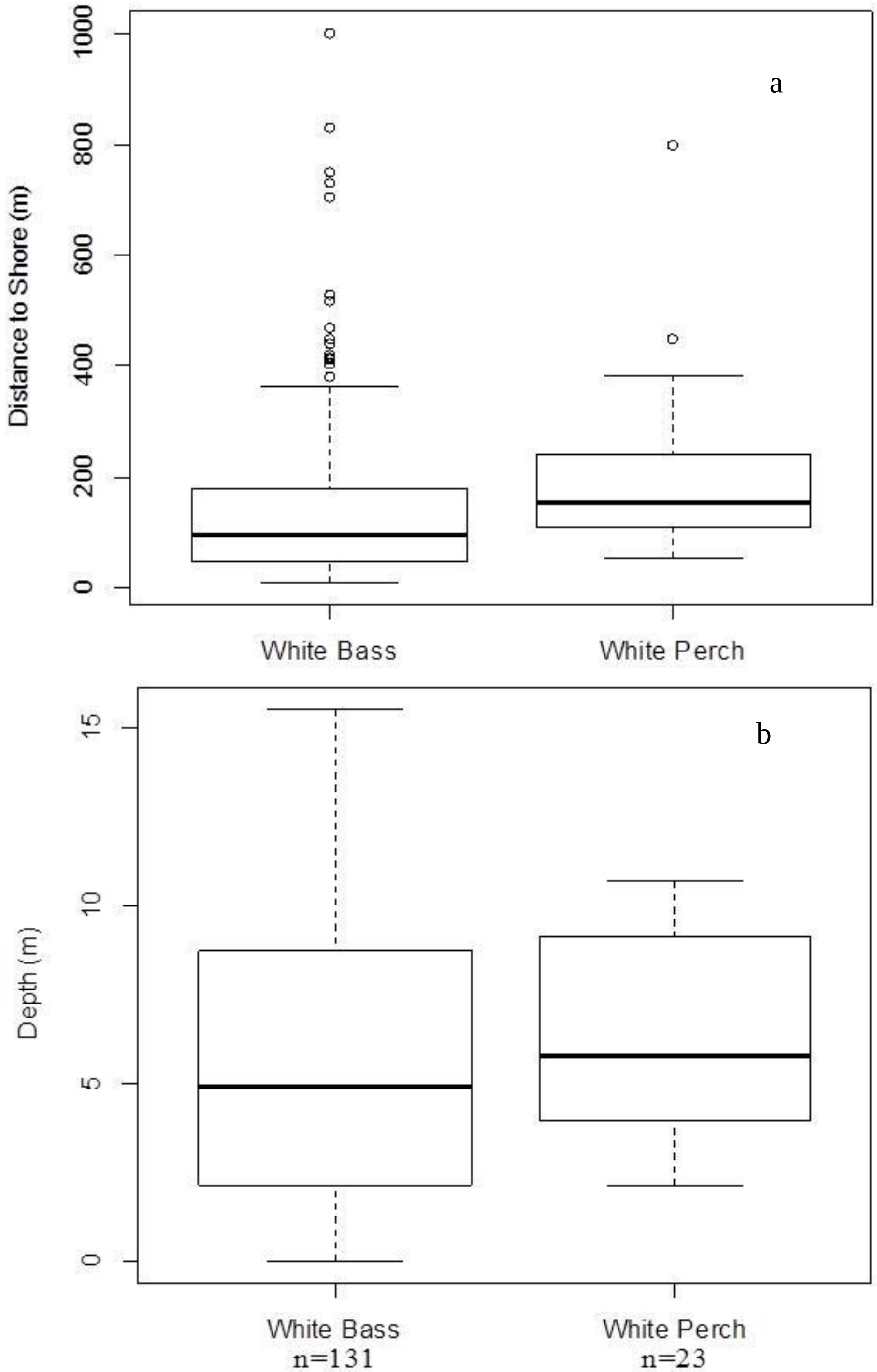

Figure 2.6: Comparisons of (a) distance to shore and (b) depth of relocated White Bass and White Perch from October 2012-May 2013; heavy lines indicate medians, boxes indicate upper and lower quartiles, bars indicate maximum and minimum values, and circles indicate outliers; n is the number of observations.

APPENDICES

Appendix A: Capture history from active and passive relocation data of White Bass from April 2012 to October 2013 and the associated tracking period (located under each month). Fish were either detected (black square), not detected (/), detected in the same location for three consecutive months and determined to have suffered a natural death (N), or never detected again and potentially harvested (H?); an * represents tags that may have expired.

	2012									2013									
	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
ID	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
4276	■	■	H?																
4277	■	■	N																
4278	/	/	■	■	■	■	■	■	■	■	■	■	■	H?					
4279	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	/	■	H?	
4280	■	H?																	
4281	■	■	■	■	■	■	■	■	■	■	■	■	H?						
4282	■	H?																	
4283	■	■	■	■	■	H?													
4284	■	■	■	■	■	■	■	■	■	■	■	■	■	H?					
4285	■	H?																	
4287	■																		
4288	■	■	■	■	■	■	■	■	■	■	■	■	■	H?					
4289	■	H?																	
4290	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	*
4292	■	■	■	■	■	■	■	■	■	■	■	■	/	/	■	H?			
4293	■	■	■	■	■	■	■	■	■	■	■	■	H?						
4295	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	H?			

Appendix A Continued

	2012									2013									
	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
ID	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
4296																			*
4297														N					
4298																			
4299														N					
4300																	/		*
4301															/		H?		
4302													H?						
4303																			
4304														N					
4305						/								N					
4306					H?														
4307							H?												
4308																			*
4309		H?																	
4310		N																	
4311				/									H?						
4313				H?															
4314		H?																	
4315													H?						
4316															H?				
4317														/	N				

Appendix A Continued

	2012								2013										
	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
ID	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
4318	■	■	■	■	■	■	■	■	■	■	■	■	■	/	N				
4319	■	■	■	■	■	■	■	■	■	■	■	■	■	H?					
4320	■	■	■	H?															
4321	■	■	■	■	■	■	■	■	■	■	■	■	■	H?					
4322	■	H?																	
4323	■	■	H?																
4324	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	*
4325	■	H?																	
8093													■	■	■	■	■	■	■
8094													■	/	■	H?			
8095													■	■	H?				
8096													■	■	■	■	■	■	■
8098													■	■	■	■	■	■	
8099													■	■	H?				
8100													■	■	■	■	■	H?	
8101													■	■	■	■	■	■	■
8102													■	■	N				
8103													■	■	■				
8104													■	H?					
8105													■	H?					

Appendix A Continued

	2012									2013									
	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
ID	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
8107														H?					
8108														H?					
8109														H?					
8110															N				
8111														H?					
8112														H?					
8113																			
8114																H?			
8115																			
8116														H?					

Appendix B: OpenBUGS code for monthly instantaneous fishing (*F*) and natural (*M*) mortality rates and detection probability (*p*) given the capture history of 19 monthly tracking periods. This code was modified from the Kery and Schaub multi-state example in the book Bayesian Population Analysis (Ch 9) and is drawn from a telemetry mortality model currently under development (J. Hightower, unpublished data).

```
model {
# Priors, constraints, and calculated values
for (t in 1:(Periods-1)){
  lnF[t] ~ dunif(-10, 10)
  lnM[t] ~ dunif(-10, 10)
  F[t] <- exp(lnF[t])
  M[t] <- exp(lnM[t])
  Z[t] <- F[t]+M[t]
  S[t] <- exp(-Z[t])
  A[t]<-1-S[t]
  u[t]<-F[t]*A[t]/Z[t]
  v[t]<-A[t]-u[t]
  }
 p[1] <- 1                     #First capture conditioned, estimate remaining p's
for (t in 2:(Periods)){
   p[t] ~ dunif(0, 1)
  }

# Define state-transition and observation matrices
  for (i in 1:nFish){
# Define probabilities of State(t+1) given State(t)
  for (t in first[i]:(last[i]-1)){
    ps[1,i,t,1] <- S[t]
    ps[1,i,t,2] <- M[t]*(1-S[t])/Z[t]
    ps[1,i,t,3] <- F[t]*(1-S[t])/Z[t]
    ps[2,i,t,1] <- 0
    ps[2,i,t,2] <- 1
    ps[2,i,t,3] <- 0
    ps[3,i,t,1] <- 0
    ps[3,i,t,2] <- 0
    ps[3,i,t,3] <- 1
    } #t
```

Appendix B Continued

```
# Define probabilities of Observed(t) given State(t). First index is state, last index is observed
  for (t in first[i]:(last[i])){
    po[1,i,t,1] <- p[t]                    #Alive, detected alive
    po[1,i,t,2] <- 0                       #Alive, natural death
    po[1,i,t,3] <- 1-p[t]                  #Alive, not detected
    po[2,i,t,1] <-  0                      #Natural mortality, detected alive
    po[2,i,t,2] <- p[t]                    #Natural mortality, detected natural mortality
    po[2,i,t,3] <- 1-p[t]                  #Natural mortality, not detected
    po[3,i,t,1] <- 0                       #Harvested, detected alive
    po[3,i,t,2] <- 0                       #Harvested, detected natural  mortality
    po[3,i,t,3] <- 1                       #Harvested, not detected
    } #t
  } #i

# Likelihood
for (i in 1:nFish){
  z[i,first[i]] <- 1                       #Alive at first occasion in study
 for (t in (first[i]+1):last[i]){
   z[i,t] ~ dcat(ps[z[i,t-1], i, t-1,])    #State process: draw State(t) given State(t-1)
    } #t
  for (t in first[i]:last[i]){
    y[i,t] ~ dcat(po[z[i,t], i, t,])       #Observation process: draw Observed(t) given State(t)
    } #t                                   #z=true state
  } #i                                     #y=Observed capture-recapture data
}
```