Biotic and abiotic factors affecting the distribution of Paddlefish *Polyodon Spathula* in William "Bill" Dannelly Reservoir and the Cahaba River, Alabama.

by

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Abstract

Paddlefish *Polyodon spathula* river section use, and summer backwater use (where zooplankton is thought to be abundant) vary seasonally. I quantified Paddlefish habitat use in Dannelly Reservoir, Alabama, which includes the confluence with the Cahaba River. I considered three longitudinal reservoir sections based on channelization and available backwater habitat, and tagged, and tracked 63 Paddlefish using both active and passive telemetry. In addition, I collected seasonal zooplankton samples across the system to quantify food availability. Zooplankton density did not differ between mainstem and backwater sites but was significantly lowest in the Cahaba River. Paddlefish detection upstream was associated with lower temperatures and higher water levels and likely represents an area critical for Paddlefish spawning. The midstream section was used year-round. The downstream section and backwaters were primarily used late spring/early fall, and backwater detections were negatively associated with food availability. I also observed limited emigration by Paddlefish from the reservoir.

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List of Abbreviations

CART	combined acoustic and radio tags
C.I.	confidence interval
df	degrees of freedom
D.S.	downstream river section
D.S.B.W.	downstream backwater
EFL	eye to fork length
MFLD	Miler's Ferry Lock and Dam
M.S.	middle river section
M.S.B.W.	midstream backwater
RFHLD	R.F. Henry Lock and Dam
S.D.	standard deviation
S.E.	standard error
U.S.	upstream river section

Introduction

Dams are prevalent on every major river globally. There are currently 91,457 impoundments in the United States, according to the U.S. Army Corps of Engineers (USACE) National Inventory of Dams (2021), with 45,177 exceeding 7.62 m in height. This number does not include small impoundments which are estimated to be between 2.6 and 9 million, exceeding 278,000 in Alabama alone (Renwick et al. 2006; Chaney et al. 2012). Dams are constructed for a variety of purposes including recreation, flood control, water supply, navigation, and hydroelectric power. As of 1995, only 42 United States rivers longer than 200 km remained unimpounded out of the nation's original 5,200,000 km of rivers (Lydeard and Mayden 1995). Dams affect habitat quantity, habitat quality, and connectivity of riverine fish populations (Cooke et al. 2002; Mettee et al. 2005; Waples et al. 2008; Jelks et al. 2008; Lapointe et al. 2014). The combination of habitat fragmentation, habitat degradation, habitat loss, and altered flows are thought to be some of greatest threats to aquatic biodiversity (Helfman 2007; Jelks et al. 2008). Even if they are passable, dams can cause injury, trauma or even death to fish attempting passage, and they may not always be passable during spawning migrations (Hoover et al. 2019).

Dams alter the natural flow and temperature regimes of a river (Poff et al. 1997; Cassie 2006; Ellis and Jones 2013). These alterations include less flow variability upstream and depending on seasonal conditions and the purpose of the dam, can further reduce or increase flow downstream. They trap sediments and alter sedimentation patterns where sediment starved waters downstream of a dam can cause increased erosion. This increased downstream erosion and sedimentation can cover previously available habitats and affect the ability of aquatic organisms to reproduce and survive (Poff et al. 1997). Reduced aquatic biodiversity has also been observed immediately downstream of dams (Travnichek and Maceina 1994; Ellis and Jones 2013; Franssen and Tobler 2013). Upstream of dams, lentic environments are created out of historically lotic environments. These controlled lentic environments have reduced interaction with the floodplain, affecting nutrient cycles (Ward and Stanford 1995). The creation of lentic environments can be beneficial for more generalist species, while leading to reductions in species that are adapted to fluvial habitats (Franssen and Tobler 2013). After impoundment, upstream tributary confluences and any low-lying areas become flooded and form reservoir arms that can accumulate coarse woody debris. This process can also create additional backwaters or expand existing backwaters. These habitats are beneficial for many fish species that thrive in low flow environments. While creating some new habitats, other habitats like rocky shoals and gravel beds often used for spawning can become submerged. In a Colorado river, species like the Fathead Minnow *Pimephales promeias* and non-native fishes dominated samples upstream of the dam in the years after dam construction and reservoir formation (Martinez et al. 1994). Marcrohabitat generalists such as Largemouth Bass *Micropterus salmoides* and Blacktail Shiner *Cyprinella venusta* can dominate reservoir habitats as reductions in fluvial specialists are observed (Herbert and Gelwick 2003). This is also true for invasive species that appear to thrive in these newly created lentic waters (Johnson et al. 2008). Although these changes in species composition have been studied, habitat use in these impoundments by many riverine fish has not been well described.

In some systems, pelagic migratory species like Paddlefish *Polyodon spathula* appear to have adapted and perhaps thrived in human created lentic environments (e.g., Paukert and Fisher 2001a). Much of the work with Paddlefish throughout their range has focused on passage at dams and seasonal migrations (Paukert and Fisher 2001b; Stancill et al. 2002; Miller and

Scarnecchia 2008, 2011; Schwinghammer et al. 2019). However, less is known about habitat use outside of spawning season nor of factors associated with that habitat use. Since the construction of dams, Paddlefish have been observed congregating in the tailraces of dams, presumably due to blockage of their historical migration routes, although they could also be using this habitat to filter zooplankton flowing in from the upstream impoundment (Southall and Hubert 1984). Paddlefish have also been observed using slow-moving areas like backwaters and oxbow lakes during summer and fall (Rosen and Hales 1981; Hoxmeier and DeVries 1997; Scarnecchia et al 2011). Paukert and Fisher (2000) found lower water levels to be associated with downstream movement by Paddlefish, and postulated they could be following a food resource, although no zooplankton samples were taken.

Objectives

Here I will use telemetry to determine the movements and factors related to habitat use of Paddlefish in William Dannelly Reservoir. I will also quantify emigration to areas below Millers Ferry Lock and Dam, above R. F. Henry Lock and Dam, and movement into the Cahaba River during upstream spawning migrations.

Specifically, I address 3 questions:

1) What is the seasonal use of different reservoir sections and associated habitat (main channel, backwater) by Paddlefish?
2) Do Paddlefish in Dannelly Reservoir move past Millers Ferry Lock-and-Dam and R. F. Henry Lock-and-dam (i.e., emigration by adult Paddlefish from the reservoir)?
3) Do Paddlefish make long distance movements and are those movements related to sex and abiotic factors?

Methods

Study Species

The Paddlefish *Polyodon spathula* is a relatively long-lived and slow-growing potamodromous species that is native to the Mississippi and Mobile river basins and coastal drainages in Louisiana and Alabama (Boschung and Mayden 2004; Pikitch et al. 2005; Jennings and Zigler 2009). The most significant threats to Paddlefish sustainability are thought to be habitat degradation and overexploitation (Jelks et al. 2008; Jennings and Zigler 2009). Paddlefish are pelagic, ram suspension filter feeders capable of long-distance spring spawning migrations (Southall and Hubert 1984; Mettee et al. 2009) that include spawning site fidelity (Hoxmeier and DeVries 1997; Lein and DeVries 1998; Paukert and Fisher 2001a; Stancill et al. 2002; Firehammer and Scarnecchia 2006; Miller and Scarnecchia 2008; Mettee et al. 2009; Simcox et al. 2015). These long-distance spawning migrations are thought to be cued abiotically by increasing temperatures (typically starting at 10°C) and pulses of discharge (Paukert and Fisher 2001a; Firehammer and Scarnecchia 2006; Miller and Scarnecchia 2008). Spawning occurs during spring high flows over gravel or cobble (O'Keefe et al. 2007; Jennings and Zigler 2009). In general, spawning periodicity for Paddlefish differs between males (every 1-2 years) and females (every 2-3 years), but in Alabama there is evidence that at least some individuals may spawn annualy (Lein and DeVries 1998; Stancill et al. 2002; Miller and Scarnecchia 2011; Paukert and Fisher 2001a; Tripp et al. 2019b). Studies have also shown seasonal variation in Paddlefish habitat selection, association with structure, and summer use of backwater habitats that are thought to be richer in zooplankton which is critical for all Paddlefish life stages (Rosen and Hales 1981; Southall and Hubert 1984; Tripp et al. 2019a). Paddlefish consume primarily crustacean zooplankton and occasionally insect larvae when in high abundances, with cladocerans and copepods representing a primary food source (Ruelle and Hudson 1977; Rosen and Hales 1981; Blackwell et al. 1995; Hoxmeier and DeVries 1997). Food availability appears to strongly affect Paddlefish early growth (Jennings and Zigler 2009; Hintz et al. 2017), particularly availability of large cladocerans (Scarnecchia et al. 2019b). As such, understanding food density patterns is vital for understanding overall population health, given that early survival and growth are both critical elements of successful recruitment (Scarnecchia et al. 2019a).

Food availability can also influence migration decisions by some fish species (Gross et al. 1988; Archer et al. 2020), and in Paddlefish it is essential for developing the fat stores needed for long-distance migrations and spawning (Scarnecchia et al. 2009; Miller and Scarnecchia 2011). Zooplankton abundance in river systems exhibits both spatial and temporal variation (Blackwell et al. 1995; Kobayashi et al. 2011; Chará-Serna and Casper 2020). Slow-moving backwater areas can be richer in zooplankton than main channels, which has been proposed as a reason for higher condition factors in Paddlefish found there (Blackwell et al. 1995; Hoxmeier and DeVries 1996). Zooplankton in rivers has also been observed reaching peak densities in spring and summer (Pace et al. 1992; Blackwell et al. 1995) and during periods of high water (Scarnecchia et al. 2009) which could influence Paddlefish movement. Zooplankton are also typically patchily distributed (Kobayashi et al. 2011; Chará-Serna and Casper 2020) and can exist in dense patches based on ecological conditions within specific sub-regions of a river (Thorp et al. 2006).

Study Area

The Alabama River forms at the confluence of the Coosa and Tallapoosa rivers. It is Alabama's longest river, with the main stem extending approximately 503 river km to the confluence with the Tombigbee River to form the Mobile River, with a 15,825 km² watershed

(Deutsch 2018). The Alabama River lies in the coastal plain physiographic region, with sediments consisting of chalk, marl, claystone, soft limestone, gravel, sands and clays (Williams et al. 2008). The coastal plain lies below the fall line which marks the steep gradient between the coastal plain and the upland physiographic provinces of the state (Williams et al. 2008).

The Alabama River has three lock-and-dam structures: Claiborne Lock and Dam (CLD), Millers Ferry Lock and Dam (MFLD), and Robert F. Henry Lock and Dam (RFHLD). Claiborne Lock and Dam, located at RKM 116, was completed in 1969 and is the furthest downstream of the three dams. CLD has a crested spillway, six flood gates, and a navigational lock chamber (U.S. Army Corps of Engineers 2015). MFLD (RKM 214) is the middle dam that creates William Dannelly Reservoir (hereafter referred to as Dannelly Reservoir) and was also completed in 1969. MFLD has 17 gates, a hydropower plant, and a navigational lock chamber (U.S. Army Corps of Engineers 2015). The dam furthest upstream on the Alabama River is RFHLD (RKM 380) which was completed in 1972 and has 11 gates, a hydropower plant, and a lock chamber.

Dannelly Reservoir (6,960 ha in Dallas and Wilcox counties) is relatively shallow (average depth = 6 m) due to the coastal plain topography (Deutsch 2018). Dannelly Reservoir lacks the characteristic dendritic shape of many reservoirs and has a relatively short residence time of water (average six days) (Deutsch 2018). Gage height in Dannelly Reservoir typically peaks in the winter through early spring. Alabama is in the humid subtropical region and average temperatures around Dannelly Reservoir reach their highest in July (33.3 °C) and lowest in January (1.9 °C) (U.S. Climate Data 2023).

The Cahaba River, a major tributary of the Alabama River, begins in the Valley and Ridge physiographic province, flowing through limestone and dolostone before crossing the fall line into the Coastal Plain where it meets with the Alabama River just south of Selma, Alabama (Williams et al. 2008). Once in the Coastal Plain, the Cahaba River substrate consists primarily of sand, gravel, and chalk (Williams et al. 2008). The Cahaba River contains Alabama's longest reach of free-flowing river that starts at the Highway 280 diversion dam in Birmingham and flows 241 km to the confluence with the Alabama River (Thom et al. 2013; Deutsch 2018). Despite the Cahaba River being mostly un-impounded, distribution of numerous species in the Cahaba River are potentially affected by the presence of lock-and-dam structures on the Alabama River that block migrating fish from moving further upriver (Thom et al. 2013).

To characterize the locations of Paddlefish relative to areas of the reservoir, I chose to divide Dannelly Reservoir into three sections based on availability of backwater habitat and channel structure (Figure 1). Compared to the other downstream sections of the reservoir, the upstream section (Section 1) between RFHLD and Section 2 is the most lotic, features the tailwaters of RFHLD and has very few backwater habitats. Section 2 remains lotic but has some interspersed small to midsized backwater habitats and includes the confluence with the Cahaba River (at RKM 303.5). The most downstream reach (Section 3) is wider, more lentic, and includes several large backwater habitats.

Fish Collection and Tag Implantation

I captured and tagged 63 Paddlefish, including 23 (2 males, 2 females, 19 unknown sex) during the 2021-22 season and 40 (20 males, 8 females, 12 unknown sex) during the 2022-23 tagging season. All fish tagged in the 2021-22 season and the first 11 fish during the 2022-23 season were collected at or downstream of the mouth of the Cahaba River and tagged and released in the same location where they were caught. This was done to reduce bias of potentially tagging all migrating fish, and this was the furthest downstream location where fish could consistently be sampled at this time of year. The remaining 29 fish during the 2022-23 season were tagged in the upper segment of the Alabama River, upstream of Selma, Alabama. Only sexually mature fish (at least 650 mm EFL; Hoxmeier and DeVries 1997) were tagged. Paddlefish were collected using a 45.72 m long and 6.71 m deep, large mesh (304.8-mm stretch) gillnet. To reduce mortality and undo stress due to length of time entangled in the net, nets were set for no longer than 2 hr and were always in sight of the boat permitting removal of Paddlefish when there was an indication that a fish was entangled. Once fish were retrieved from the net, they were placed in a holding tank prior to tagging. Before surgery, fish were weighed (nearest g) and measured (nearest mm, eye-to-fork length [both flat and curved], block length, and girth). Sex was determined by the presence of tubercules or by the presence of oocytes during surgery.

Fish were surgically implanted with a combined acoustic and radio transmitter (LOTEK Wireless CART tag model MM-MC-16-50), that included temperature and pressure sensors and transmit a signal every 10 seconds. Tags did not exceed 2% of the fish’s body weight (Winter 1996; Cooke et al. 2012). These tags transmit a radio and acoustic signal every 10 seconds, and they were inserted through an approximately 2-cm incision that was then closed using a combination of interrupted sutures and 3M Vetbond veterinary adhesive. Incisions were made on the left ventral side just anterior to the pelvic girdle (Hershey 2019; Thomas et al. in press; Hershey et al. 2021). Water was continuously pumped over the animal’s gills during surgery. Surgery time was kept to approximately 2 min, and all surgical instruments and tags were sterilized in chlorhexidine. Uniquely numbered anchor tags were inserted on the right ventral side to ensure identification should the fish be recaptured. After surgery, fish were allowed to recover in the holding tank and released once equilibrium was regained. GPS coordinates were recorded to mark the release site, which was within 100 m of the capture locations.

Stationary Acoustic Telemetry

An array of 12 Lotek acoustic receivers (model WHS 3250L) was deployed in Dannelly Reservoir's main channel, with 4 located in each of the 3 sections (Figure 1). I attempted to space the receivers approximately equally (~15 km), and selected sites that allowed for retrieval of the receiver and assured the receiver would detect a fish across the width of the river. Additional receivers (n = 17) were located downstream of Miller's Ferry Lock and Dam (16 receivers) and just upstream of R. F. Henry Lock and Dam (1 receiver) to allow detection of any fish leaving Dannelly Reservoir. Using satellite images from Google Earth (https://earth.google.com), I identified 67 backwater areas on Dannelly Reservoir, most of which were concentrated in the lower third (Section 3) with some smaller backwaters in the middle third of the river (Section 2). I visited each identified backwater site to determine both accessibility for Paddlefish and suitability for receiver placement. Backwaters were defined as sloughs, lentic arms of the reservoir, and intermittent or low current velocity off channel areas connected to the main stem of the river (Southall and Hubert 1984). This included flooded creek channels created by the reservoir. Backwater sites were evaluated by examining maximum depth and depth at the backwater's connection to the main reservoir during the average low period. If a backwater was mostly shallow (< 2 m), too shallow at the connection to the reservoir to be accessible to fish year-round or did not have a location where a receiver could be deployed that prevented detections by the receiver of fish in the main channel, it was excluded from consideration for receiver placement. I identified six suitable backwater sites in Section 2, and 20 suitable sites in Section 3. I then used a random number generator to select 5 suitable sites from Section 2 and two suitable sites from Section 3 (Figure 1). In addition, I had already preselected three sites in Section 3 based on the observed presence of Paddlefish while scouting sites which were added to the 2 randomly selected sites noted above (Figure 1). Receivers were installed in all 10 backwater locations. I also installed three receivers in the Cahaba River, one near the US-80 bridge (approximately 34 RKM from the confluence with the Alabama River), one near the Highway 22 bridge (approximately 12 RKM from the confluence), and one just upstream of the confluence with the Alabama River (Figure 1). Due to a lack of accessibility throughout the study period, only the lower two receivers could be maintained. All other receivers were downloaded, and batteries changed every 4 months.

Manual Tracking

Manual tracking was conducted twice per season (winter = December – February, spring = March – May, summer = June – August, Fall = September - November) from December 2021 through September 2023 to supplement stationary receiver detection data. A three-bar Yagi antenna was used in combination with a Lotek SRX 800 radio receiver (gain set to 70) while navigating a boat at approximately 22 km/hr. When a fish was first detected, the boat speed was reduced, and I began using a Lotek AcouTrack acoustic receiver. The acoustic receiver includes two hydrophones, one placed on each side of the boat, to provide more precise location and reception of the pressure and temperature data transmissions. Each tracking event was concluded when either all fish were located, or the entire study area was covered. The study area included the entire main channel of Dannelly Reservoir, backwater sites, and up to the most upstream Cahaba River receiver location. The backwaters and arms of the lower portion of the reservoir that did not contain a receiver were not tracked unless a fish was detected there from the main channel.

Tag Testing

To check the pressure and temperature values I was getting in the field, I conducted a test in a pond at the E.W. Shell Research Center, Auburn, Alabama. A stationary receiver was deployed in the pond, and the manual acoustic receiver was used from a boat. I then deployed a tag at 0.5 m increments from 0 m to 4.0 m approximately 30 m from the stationary receiver. The tag remained at each 0.5 m increment until the manual tracker detected it at least 10 times. Temperature readings were also taken at each depth with a YSI Pro 20. Once complete, I compared the YSI readings, the known depth, the stationary receiver readings, and manual receiver readings to confirm accuracy of the readings using an analysis of variance (ANOVA).

Gage Height

Because discharge is not available from the United States Geological Survey (U.S.G.S. 2023) gages in Dannelly Reservoir, daily and weekly percent changes in gage height were used as a surrogate for discharge. There are two gaging stations in the upper portion of Dannelly Reservoir, one at Selma, Alabama and the other just below R. F. Henry Lock and Dam. The Selma gage was used because it is close to the confluence with the Cahaba River and therefore better reflects water conditions in the reservoir away from R. F. Henry Lock and Dam. For the weekly percent change in discharge, the first gage height of the week on Sunday was subtracted from the last gage height of the week on Saturday, then divided by the starting value, and multiplied by 100. Daily percent change in gage height was calculated by subtracting the average gage height from the subsequent day's average gage reading, dividing by the previous day's average value, and multiplying by 100.

Zooplankton Sampling

To quantify food availability in the study area, each of the three reservoir sections was divided into two sub-regions for zooplankton sampling (Figure 1). Due to year-round accessibility issues, only the lower receiver site of the Cahaba River was sampled. All backwater areas with a stationary receiver were also sampled. Zooplankton samples were taken once per season. At each site, 3 replicate samples were taken by lowering a plankton net to twice the observed Secchi depth (to incorporate the photic zone) and slowly pulled to the surface. The conical plankton net was 300-mm diameter, 1050-mm long, with 100-µm mesh. Mesh size was selected to incorporate zooplankton sizes consumed by Paddlefish, (Rosen and Hales 1981). Vertical plankton tows were used to provide a vertically integrated sample. Dissolved oxygen readings (YSI Pro 20) were also taken at all zooplankton sampling sites. Samples were preserved in 95% ethanol and transported to the lab. Zooplankton were subsampled until a minimum of 200 of the most common taxa was counted (Dettmers and Stein 1992; Welker et al. 1994). Zooplankton were identified to genus for cladocerans and to family for copepods. If macroinvertebrates occurred in samples, they were also identified, measured, and counted. A subsample (n=10) of individuals from each taxon from each subsample was measured. Two replicate subsamples were quantified if values were within 30%, otherwise the third sample was also quantified.

Data Analysis

All analyses were performed in Rstudio (version 2023.06.2, Rstudio Team 2023). To obtain total zooplankton density, replicate subsample counts were extrapolated to the whole sample, volume of water filtered was used to calculate density, and density values were averaged across replicates. Zooplankton density in the main channel was compared to that in backwater habitats across the reservoir using a Wilcoxon Ranked Sum Test. I used a Kruskal-Wallis Test to compare zooplankton density across sections, given that the data were not normally distributed. I then performed a Dunn test with Bonferroni correction to determine any significant differences between sections. The same tests were used to determine if zooplankton density differed across seasons.

Paddlefish detection data were filtered to minimize the potential for false detections. Each individual had to be detected at least twice by a passive receiver on a given date or it was not retained in my data set. Manual tracking data were manually sorted by locating the highest strength detection (as it provides the most accurate temperature and pressure reading), and then merged with the passive receiver data. Each detection was assigned to a reservoir section based on the receiver location. Because each section has four receivers and two zooplankton sites, two receivers per section were assigned each a zooplankton site. The furthest two upstream receivers within the section were assigned to the section's upstream zooplankton site, and the furthest two downstream receivers were assigned to the section's downstream zooplankton site. All backwater sites and the Cahaba River were assigned to their individual zooplankton sampling site. The average zooplankton density for each sampling event at each site was then merged with the fish detection data. Gage data were incorporated as both daily and weekly percent changes in gage height that were assigned to the date for each detection.

Covariates considered for the analysis included daily and weekly percent change in gage height, gage height on the day of the detection, release location, sex, zooplankton density, average daily temperature and average daily water depth from the tag sensors, eye-to-fork length, weight, and girth. Generalized linear mixed models (GLMM) were built using the glmmTMB (Brooks et al. 2017) package in R to determine which factors were correlated with Paddlefish location (defined by main channel sections and backwaters) throughout the entirety of the study (Bolker et al. 2008). All numerical covariates were centered and scaled so that their mean = 0 and standard deviation = 1 to facilitate model convergence and interpretation of results. For each reservoir section a new column was created in the data matrix which had a 1 indicating if that section was being used and a 0 if it was not, and separate GLMMs were run using a binomial distribution where each reservoir section was the response variable. Once a full model was constructed, the MuMIn package in R (Bartoń 2023) was used for automated model selection and comparison. The DHARMa package (Hartig 2022) was then used to verify there was no overdispersion, and no outliers, and a Q-Q plot was used to assess model fit. The top model was then selected based on the AICc rating and how parsimonious the model was. If multiple AIC ratings fell within 2 points of each other, the most parsimonious model was chosen. Detections were also filtered to unique days on which an individual was detected and then summed by reservoir section and habitat (mainstem sections, backwaters) to determine the number of days an individual was detected in each reservoir section and habitat. I then performed a Kruskal-Wallis Test to determine if there was a difference in location between sexes (Kruskal and Wallis 1952). A Dunn's Test with a Bonferroni correction on significant results of the Kruskal-Wallis Tests was then performed to determine if males, females, and unknown sex fish differed in habitat use (Dunn 1964).

Results

Zooplankton

Zooplankton densities differed among reservoir sections (Kruskal-Wallis $\chi^2 = 42.24$, $p < 0.001$), being lower the Cahaba River than each of the other sections (Dunn's test; z range: -3.47 to -4.16, $p < 0.001$ for each pairwise comparison) (Figure 2). No other comparisons were significant. Zooplankton density did not differ between mainstem and backwater sites (Wilcoxon rank-sum test; W = 1165, p = 0.087), but did differ across seasons (Kruskal-Wallis $\chi^2 = 67.84$, p < 0.001), being higher in fall than spring (Dunn's test; z = 5.16, p < 0.001) and winter (Dunn's test; z = 6.43, p < 0.001), and higher in both spring (Dunn's test; z =5.087, p < 0.001) and winter (Dunn's test; z = 6.35, p < 0.001). There were no differences between summer and fall. The most abundant taxa in the main channel were *Bosmina* and cyclopoid copepods, although in the summer and fall copepod nauplii was also present in high densities, particularly in the upstream section and midstream backwaters.

Tag Testing

I collected 106 temperature and 100 depth detections using the manual tracker and 31 temperature detections and 31 depth detections from the stationary receiver from the 9 tested depths of the stationary tag during the pond test. Neither temperature (F = 2.47, df = 2, p = 0.09), nor depth (F = 20, df = 2, p = 0.82) differed across any of the measures.

Section Use

I had a total of 6,754,169 detections of tagged fish on either passive receivers or during manual tracking. The total number of days of detection of individual fish was 6,718 (detection days). All 63 fish were detected during the study. The mean (± S.D.) number of days individual fish were detected was 106.63 ± 79.59 (range = 2 – 323, n = 63). No fish were detected passing above RFHLD, and only 2 individuals were detected below MFLD. Of the 3 mainstem sections, the middle section had the highest detection days (3,123, range = 0 – 229, n = 57 fish) followed by the upstream section (1,287 detection days, range = 0 - 168, n = 42 fish), and the downstream section (1,106, range = 0 – 134, n = 32 fish. Six individuals were detected entering the Cahaba River, generating 22 detection days (mean ± S.D. = 0.35; ± 1.27) (Figures 3 - 5). Paddlefish did not appear to avoid hotter temperatures by using deeper waters in the summer months (Figure 6). Male and female Paddlefish appeared to show more typical upstream – downstream migration patterns (Figure 7 and 8), while unknown sex fish did not (Figure 9).

Given that all AICc scores for the upstream section detection model were within 2 and, therefore insufficient to fully separate models, model selection criteria included model weight, and the model being parsimonious. This model included gage height, temperature, release location, zooplankton density, girth, and weight (Table 1). Zooplankton density was negatively correlated with presence in the upstream section ($\beta = 0.66$, 0.53 - 0.81 C.L., $p < 0.001$). Paddlefish were more likely to be present in the upstream section of the reservoir when the gage height was higher ($\beta = 1.043$, 1.012 - 1.074 C.L., $p = 0.006$). Temperature was negatively related to presence in the upstream section ($\beta = 0.14$, 0.12 - 0.17 C.L., $p < 0.001$). Fish released near Selma were more likely to be detected in the upstream section than fish released near the Cahaba River, but there was a lot of uncertainty associated with that relationship ($\beta = 1.68e+4$, 4.086e+4 – 6.91e+5 C.L., $p < 0.001$). Fish detected in the upstream section had larger girth ($\beta = 378.11$, 1.76 – 8.13e+4 C.L., $p = 0.03$) but weighed less ($\beta = 0.0013$, 5.58e-6 – 0.28 C.L., $p = 0.016$) at the time of tagging.

Presence of Paddlefish in the midstream section was associated with all covariates except gender and the body size metrics (Table 2). Zooplankton density showed a positive correlation with presence in the midstream section ($\beta = 1.97$, 1.75 – 2.21 C.L., $p < 0.001$). Gage height ($\beta = 0.92$, 0.89 – 0.95 C.L., $p < 0.001$) and daily percent change in gage height ($\beta = 0.87$, 0.81 – 0.93 C.L., $p < 0.001$) were negatively correlated with the midstream section. Weekly percent change in gage height had a positive correlation with presence in the midstream section ($\beta = 1.079$, 1.0024 – 1.16 C.L., $p = 0.043$). Lower temperatures ($\beta = 0.63$, 0.57 – 0.70 C.L., $p < 0.001$) and fish use of deeper depths (β = 1.15, 1.073 – 1.24 C.L., $p < 0.001$) were associated with Paddlefish presence in the midstream section. Fish released upstream of Selma were less likely to be detected in the midstream section than fish tagged near the Cahaba River (β = 0.036, 0.0069 – 0.19 C.L., $p < 0.001$).

Body metrics of Paddlefish led to the residuals in the downstream model to be overdispersed and have significant outliers, so they were removed from the analysis. The model for the downstream section only excluded release location given that it was not a significant factor (Table 3). After fitting the model, daily percent change was not a significant variable, so it was removed for the model. Females were more likely to use the downstream section compared to unknown sex individuals (β = 0.0012, 5.72e-5 – 0.027 C.L., $p < 0.001$). Zooplankton density was positively associated with downstream detections (β = 1.48, 1.31– 1.68 C.L., $p < 0.001$). Gage height had a negative correlation with downstream detections (β = 0.94, 0.91 – 0.96 C.L., $p < 0.001$), while weekly percent change in gage height had a positive correlation (β = 1.12, 1.049 – 1.20 C.L., $p < 0.001$). Higher temperatures (β = 1.14, 1.036 – 1.24 C.L., p = 0.0065) and deeper depths were also associated with downstream detections (β = 1.48, 1.39 – 1.58 C.L., $p < 0.001$).

Use of different reservoir sections by the different sexes differed significantly for the midstream section ($\chi^2 = 7.002$, d.f. = 2, p = 0.03), the downstream section ($\chi^2 = 15.29$, d.f. = 2, $p < 0.001$), and the downstream backwaters ($\chi^2 = 9.83$, d.f. = 2, p = 0.0073). Females were detected less often and had fewer detection days in the midstream section than unknown sex individuals (Dunn's Z = -2.34, p = 0.029), but all other comparisons were not significant. Both males and females were detected more in the downstream section than unknown sex individuals (females: Dunn's Z = 3.41, $p < 0.001$; males: Dunn's Z = 2.9, p = 0.0057) (Figures 3 - 5). Males were also detected in the midstream backwaters less than unknown sex individuals (Dunn's Z = -3.04, $p = 0.0036$).

Backwater Use

There were 1,115 (n = 22 fish) detection days for Paddlefish in backwaters with 74 (n = 11 fish) in the midstream section and 1,041 (n = 17 fish) in the downstream section. The mean number of days during which an individual fish was detected was 1.17 (± 4.58 S.D.) in the midstream backwaters and 16.52 (± 48.76 S.D.) in the downstream backwaters. Downstream backwaters had the highest number of individuals detected during spring through fall, and individuals in midstream backwaters were only detected during winter and spring (Tables 4 and 5). Males were detected in backwaters on 334 days (n = 7 individuals) and used backwaters an average of 15.77 days (± 38.42 S.D.) during the study period. Females were detected in backwaters 308 days (n = 4 individuals), and their average backwater use was 31.5 days (± 55.04 S.D.). There were 473 backwater detection days (n = 11 individuals) for unknown sex fish with a mean of 15.71 days (± 55.04 S.D.). The most visited backwater sites had from 19-513 detections days by 4 – 9 unique fish (Table 6).

The GLMM selected using AICc criteria for backwater habitats included zooplankton density, gage height, weekly change in gage height, temperature, depth, weight, and girth (Table 7). Zooplankton density was negatively related to backwater detections ($\beta = 3.91e\text{-}4$, 0.00018 – 0.00087 C.L., $p < 0.001$). Gage height was positively correlated with backwater detections ($\beta = 1.14$, 1.091 – 1.20 C.L., $p < 0.001$). Weekly percent change in gage height was negatively correlated to backwater detections ($\beta = 0.51$, 0.43 – 0.61 C.L., $p < 0.001$). Fish using backwaters experienced higher water temperatures ($\beta = 94.68$, 62.91 – 142.47 C.L., $p < 0.001$) and used shallower depths ($\beta = 0.45$, 0.38 - 0.53 C.L., $p < 0.001$) compared to detections elsewhere. Fish that were detected in backwaters were heavier ($\beta = 1.44e+4$, 1.55 – 1.33e+8 C.L., $p = 0.040$) but had smaller girth ($\beta = 1.24e-4$, 1.075e-8 – 1.44 C.L., $p < 0.001$) at the time of tagging.

Spawning Migration

During the spring 2022 spawning season, one tagged fish was found in the tailrace of RFHLD and two fish entered the Cahaba River while temperatures were between 10-17°C (Table 8). I also found that two out of the 23 fish were in a ~21 km area starting around RKM 356 of the river (Table 8) which potentially represents spawning habitat (Figures 1, 10, and 11). All other fish (n = 19) remained in the midstream section and the lower portion of the downstream section. During the spring 2023 spawning season, eight of 51 individuals detected during that time were found in the tailrace of RFHLD, 28 were in RKM 356 - 375, and four entered the Cahaba River (Table 8). Females and males were first detected at each of these three potential spawning habitats within a day of each other, except for RKM 356 – 375 in the spring 2022 where a female was detected 16 days after a male arrived. In this instance, the tagged male and female fish were not detected in the area during the same time period, and the end dates were within 1 day of arrival. In the second season at the RFHLD tailrace, one female was present for 18 days, while one male was only detected for 2 days. In the Cahaba River, tagged male and female fish were not present at the same time.

Discussion

Paddlefish did not always move or use habitat as would have been expected based on what has been reported in the literature. My first study question related to quantifying seasonal use of section/areas of the reservoir by Paddlefish, and the factors associated with detections there. Many of the fish tagged in the middle reservoir section, near the confluence with the Cahaba River, during the first spawning season did not move directly upstream and then directly back downstream as would have been expected based on previous work (Stancill et al. 2002; Miller and Scarnecchia 2009; Hershey et al. 2022). Furthermore, most of the fish tagged there did not have tubercules or presence of oocytes that would indicate spawning condition, despite being near the time of their spawning window. Fish having larger girth at the time of tagging being positively associated with detections in the upstream section is further indirect evidence of tagged fish migrating to spawn. Most fish I could positively identify as female through presence of eggs (7 of the 10) were tagged in the upstream section and could be what is driving this result. The upstream section of the reservoir was mostly used by Paddlefish during winter and spring, with some individuals remaining there during summer in 2022. Zooplankton density was not associated with upstream section use and did not support the suggestion that Paddlefish in tailwaters may be congregating there to filter zooplankton from the upstream reservoir (Southall and Hubert 1984). Increased gage height being associated with detections in this section, while lower gage height was associated with detections in the midstream and downstream sections, are consistent with previous observations that temperature and higher water levels cue Paddlefish upstream migrations (Schwinghammer et al. 2019; Tripp et al. 2019b).

Paddlefish, particularly unknown sex individuals, used the middle river section throughout the year. Mettee et al. (2009) found that over half of the tagged fish tagged in the next downstream Alabama River reservoir remained in that reservoir, while the rest migrated past the downstream dam. This is a similar behavior to what I observed, except fish in my study had little opportunity to pass the downstream dam. During winter, Paddlefish in the Missouri River have been noted to congregate below the confluence with the Yellowstone River (Scarnecchia et al. 2011). This behavior was suggested to be a result of decreased oxygen demands during colder temperatures making mid-reservoir areas in the mainstem more favorable than the slower moving waters of the lower reservoir (Scarnecchia et al. 2011). Stancill et al. (2002) also observed Paddlefish congregating in the Missouri River near the confluence of the White River during spring and suggested that it was a result of fish responding to environmental cues such as water temperature and flow. I also observed fish congregations at or just upstream of the mouth of the Cahaba River during winter. The lower temperatures and increasing weekly gage height associations with midstream section detections I found agree with environmental cues contributing to presence there. In other seasons, presence in the midstream section could be a combination of factors, including comparable food availability relative to other sections, and reduced migration distance for those fish that are migrating. This year-round mid-reservoir presence may indicate the possibility of spawning periodicity (i.e., some individuals spawning in alternate years) in this population (Lein and DeVries 1998; Paukert and Fisher 2001 a, b). Thus, an alternative hypothesis could be that the high numbers of unknown sex individuals found there were not actively spawning, and due to adequate food availability had no need to travel into the more lentic downstream section to avoid higher flows.

The Paddlefish I tagged were detected in the downstream section more frequently during late spring through early fall, than during other seasons, which also coincided with the timing of increased backwater use in the downstream section of the reservoir. Most Paddlefish that used the downstream section left it by mid-fall, which differs from the findings of Stancill et al. (2002) who found that Paddlefish congregated in lower reservoir reaches during winter. The tagged fish in my study identified as male or female, on average, displayed more typical upstream-downstream migration behavior than did unknown sex fish, leading to higher rates of detection of male and female fish in the downstream section than unknown sex fish. Paukert and Fisher (2000) suggested food availability likely played a role in Paddlefish movements.

Interestingly, Paddlefish movements in Dannelly Reservoir do not appear to be solely a function of food availability, given that food availability did not differ across the three mainstem sections (similar to Blackwell et al. 1995). Rather, it may be that a combination of factors meets an individual's needs at a given time of year. The positive correlation of zooplankton density and downstream detections aligns with the peak zooplankton densities found during summer and fall which are times when fish used this section. Paddlefish use of the downstream section may be a function of available food resources during non-spawning seasons, combined with presence/availability of backwaters, and the generally more lentic nature of the downstream section, providing some refuge from flow after fish have migrated from the reservoir up to RFHLD and then back downstream.

Paddlefish in other systems have been observed to use backwater habitats more heavily than mainstem habitats during summer (Scarneccia et al. 2011). Interestingly, the only time the midstream backwaters were used here was during winter and spring, and even then, they were only briefly used. The downstream backwaters saw far more use than midstream backwaters, and fish used these backwaters for longer periods of time. These habitats were primarily used during late spring through early fall, consistent with previous work (Hoxmeier and DeVries 1997; Scarnecchia et al. 2011). I detected 4 fish that each used backwaters more than 100 days, with one individual tagged in the first year being detected in backwaters 296 days and another tagged in 2023 already having spent 117 days in backwaters. I did not observe a higher percentage of fish in backwater habitats versus mainstem habitats during summer, however. There were 11 fish that were not detected during summer for a month or more after entering the downstream section, that were later detected again. Given that I did not detect them in the mainstem during manual tracking efforts, there is a strong possibility that these fish were using one of the many backwaters available in this section (most of which did not have receivers). More extensive tracking of backwater habitats may reveal an even higher proportion of Paddlefish using these habitats during the summer.

Zooplankton density was not positively associated with backwater use which has previously been suggested as being a contributing factor in backwater residency (Rosen and Hale 1986; Blackwell et al. 1995; Scarnecchia et al. 2011). I did not find any difference in zooplankton density between the mainstem and backwater sites, contrary to the findings of Blackwell et al. (1995) who found significantly higher zooplankton densities in backwaters during the summer. Backwater habitat use may represent the best choice of habitat use in Dannelly Reservoir for several reasons. First, the low flow environment could act as a refuge from excess activity constantly required in moving waters during thermally stressful periods. Second, adequate food availability in backwater habitat could provide an opportunity for fish growth. By maximizing their growth potential and prey encounter rates in a habitat with limited prey loss to flow, Paddlefish would likely improve their survival, ability to migrate, and reproductive potential (i.e., their fitness) (Brandt and Kirsch 1993; Goyke and Brandt 1993; Leone et al. 2012).

My second study question related to the extent of movements above and below the reservoir. I detected only 1 male and 1 female fish passing below Millers Ferry Lock-and-Dam, and no fish passed above R.F. Henry Lock-and-Dam. This, combined with previous findings on the Alabama River below Miller’s Ferry Lock and Dam (Mettee et al. 2009, Simcox et al. 2015), supports that the population between these two dams may be isolated from the population below Millers Ferry Lock-and-Dam which is consistent with conclusions of Kratina et al. (2023) based on a microchemical analysis of fish hard parts. To fully determine how isolated these populations of Paddlefish are from one another, downstream movement (or lack of same) of both adults and juveniles will need to be more fully quantified. Such habitat fragmentation can lead to genetic bottlenecking in populations (Schwemm et al. 2019), although such an effect is not yet evident in such a long-lived fish population on the Alabama River (Kratina et al. 2023). However, modeling of the Paddlefish metapopulation on the Alabama River suggested that improved downstream passage at these structures may be necessary to maintain long-term population sustainability (Hershey 2023).

My third study question addressed potential long-distance movements by Paddlefish, including effects of sex and whether these migrations included the Cahaba River. Previous work on the Alabama River, both below MFLD and above RFHLD, has observed Paddlefish congregating in the tailraces of dams during spawning season (Lein and DeVries 1998; Mettee et al. 2009; Simcox et al. 2019; Hershey et al. 2022; Thomas et al. in press), a behavior that has also been observed in other systems (Southall and Hubert 1984; Stancill et al. 2002; Jennings and Zigler 2009). And Lein and DeVries (1998) also observed Paddlefish in the Cahaba River during spawning season. While fish in my study used both the Cahaba River and the RFHLD tailrace, far more individuals were found around several upstream gravel beds (RKM 356 – 375) during peak spawning temperatures. This area of the river may represent habitat for Paddlefish reproduction in Dannelly Reservoir, and future work should focus on quantifying use of and potential spawning in these areas. In the Mobile River basin, temperatures associated with Paddlefish spawning migration have been documented to be 10.1- 17.1°C in the Tallapoosa and Cahaba rivers (Lein and DeVries 1998), 10-23°C in the lower Alabama River (Hoxmeier and DeVries 1997), and 16.9-19.4°C in the Tombigbee River (O'Keefe et al. 2007). The temperatures observed at potential spawning habitats in this study, (9.42-24.8°C), are generally consistent with previous observations. I did not see a strong trend of either sex arriving at or staying longer in potential spawning locations as has been observed in other systems (Stancill et al. 2002, Miller and Scarnecchia 2011, Schwinghammer et al. 2019), but my sample size of known sex individuals was relatively small.

Also of note, I found the invasive *Daphnia lumholtzi* at all 17 sampling sites (Havel and Herbert 1993), with their highest densities being in the downstream backwater sites during summer 2022 where they contributed most of the zooplankton present. Their presence may be beneficial for Paddlefish (Eachus 2015), but their effects on other native aquatic vertebrates and invertebrates can be mixed (Johnson and Havel 2001; Celik et al. 2002). Mussel glochidia were also in high enough densities to be detected in our sampling, which could be a potential positive sign for mussel conservation, although species that are contributing would need to be identified.

Conclusions

In this system, food availability does not appear to be the sole determining factor in where Paddlefish spend their time. For fish found in the upstream section during winter and spring, it appears likely that they are moving there to spawn, and there is an abundance of habitat present for them to do so. Gravel beds found in this river section need to be investigated in the spring for indicators of spawning activity. High water and cold temperatures are associated with detections in upper reservoir reaches of Dannelly Reservoir. The similar density of zooplankton in the middle river section relative to other parts of Dannelly Reservoir, combined with a shortened spawning migration may be a reason we see Paddlefish here year-round. This is also where the confluence with the largely unimpounded Cahaba River is, and something about this confluence attracts large groups of Paddlefish during winter and spawning migrations. The downstream reservoir section and its associated backwaters are used primarily during late spring through early fall, and the lentic nature of this river reach, combined with food availability peaking in summer and fall likely provide refugia from flow with adequate food for fish that have completed their migrations. Immigration and emigration of fish across either Miller's Ferry Lock and Dam or R.F. Henry Lock and Dam appear to be extremely rare during my study period, this population is likely mostly self-contained. However, it is important that downstream passage of adults and juvenile Paddlefish be more fully quantified to determine the importance of this movement to population dynamics. Understanding the connectivity among the mostly isolated Paddlefish populations in the Alabama River is important for determining the sustainability of Paddlefish in the Alabama River given that improved connectivity between Paddlefish populations in the Alabama River may needed for long term population stability.

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Tables

Table 1. AIC table for GLMM evaluating factors associated with upstream section use by Paddlefish in Dannelly Reservoir. Factors are daily percent change in gage height, depth, gage height, fish girth, fish length, release location, fish sex, temperature where the fish was detected, weekly % change in gage height, fish weight, and zooplankton density. Degrees of freedom for each model, AIC score, change in AIC, and model weight are also included.

Intercept	Day chg.	Depth	Gage	Girth	Length	Rls.	Sex	Temp.	Wk. chg.	Weight	Zp.density	df	logLik	AIC	delta	wt.
0.000018	1.068	NA	1.04	368.54	NA	+	NA	0.14	NA	0.0013	0.65	9	-1378.57	2775.14	0.00	0.05
0.000017	NA	NA	1.04	378.11	NA	+	NA	0.14	NA	0.0013	0.66	8	-1379.68	2775.36	0.22	0.04
0.000018	1.066	0.93	1.04	382.69	NA	+	NA	0.14	NA	0.0012	0.65	10	-1377.79	2775.58	0.44	0.04
0.000011	1.068	NA	1.04	NA	6.47	+	NA	0.14	NA	0.0001	0.65	10	-1377.84	2775.69	0.54	0.04
0.000016	NA	0.93	1.04	392.61	NA	+	NA	0.14	NA	0.0012	0.65	9	-1378.85	2775.70	0.56	0.04
0.000010	NA	NA	1.04	NA	6.42	+	NA	0.14	NA	0.0001	0.66	9	-1378.96	2775.91	0.77	0.03
0.000011	1.066	0.93	1.04	NA	6.47	+	NA	0.14	NA	0.0001	0.65	11	-1377.06	2776.12	0.98	0.03
0.000010	NA	0.93	1.04	NA	6.43	+	NA	0.14	NA	0.0000	0.65	10	-1378.12	2776.25	1.10	0.03
0.000018	1.069	NA	1.04	NA	NA	+	NA	0.14	NA	NA	0.65	7	-1381.44	2776.88	1.73	0.02
0.000001	1.068	NA	1.04	NA	NA	+	+	0.14	NA	0.0007	0.65	11	-1377.45	2776.89	1.75	0.02
0.000000	NA	NA	1.04	NA	NA	+	+	0.14	NA	0.0007	0.66	10	-1378.56	2777.11	1.97	0.02
0.000018	1.068	NA	1.04	368.75	NA	+	NA	0.14	0.00	0.0013	0.65	10	-1378.57	2777.14	2.00	0.02

Table 2. AIC table for GLMM evaluating factors associated with middle section use by Paddlefish in Dannelly Reservoir. Factors are daily percent change in gage height, depth, gage height, fish girth, fish length, release location, fish sex, temperature where the fish was detected, weekly % change in gage height, fish weight, and zooplankton density. Degrees of freedom for each model, AIC score, change in AIC, and model weight are also included.

Intercept	Day chg.	Depth	Gage	Girth	Length	Rls.	Sex	Temp.	Wk. chg.	Weight	Zp.density	df	logLik	AIC	delta	wt.
19.02	0.87	1.15	0.92	NA	0.59	+	NA	0.63	1.08	NA	1.97	10.00	-3147.69	6315.37	0.00	0.12
21.25	0.87	1.15	0.92	NA	NA	+	NA	0.63	1.08	NA	1.97	9.00	-3148.75	6315.50	0.13	0.11
17.36	0.87	1.15	0.92	NA	NA	+	NA	0.63	1.08	0.64	1.97	10.00	-3148.22	6316.45	1.08	0.07
18.09	0.87	1.15	0.92	0.68	NA	+	NA	0.63	1.08	NA	1.97	10.00	-3148.34	6316.67	1.30	0.06
21.62	0.87	1.15	0.92	NA	0.43	+	NA	0.63	1.08	1.52	1.97	11.00	-3147.57	6317.14	1.76	0.05
4.66	0.87	1.15	0.92	NA	NA	+	+	0.63	1.08	NA	1.96	11.00	-3147.59	6317.17	1.80	0.05
20.33	0.87	1.15	0.92	1.28	0.50	+	NA	0.63	1.08	NA	1.97	11.00	-3147.62	6317.24	1.87	0.05

Table 3. AIC table for GLMM evaluating factors associated with downstream section use by Paddlefish in Dannelly Reservoir. Factors are daily percent change in gage height, depth, gage height, fish girth, fish length, release location, fish sex, temperature where the fish was detected, weekly % change in gage height, fish weight, and zooplankton density. Degrees of freedom for each model, AIC score, change in AIC, and model weight are also included.

Intercept	Day chg.	Depth	Gage	Rls.	Sex	Temp.	Wk. chg.	Zp.density	df	logLik	AIC	delta	wt.
4.4	1.058	1.49	0.93	NA	+	1.12	1.11	1.48	10	-3660.99	7341.98	0.00	0.38
8.8	1.058	1.49	0.93	+	+	1.13	1.11	1.48	11	-3660.64	7343.28	1.30	0.20
3.94	NA	1.48	0.94	NA	+	1.14	1.12	1.48	9	-3662.64	7343.29	1.31	0.20

Table 4. Number of individual Paddlefish detected at each downstream Dannelly Reservoir backwater site for each season during the study period.

Downstream		Backwater Site				
Season	Numbers of Unique Individuals	4001	4002	4003	4004	4005
Winter 2021	0	0	0	0	0	0
Spring 2022	5	0	1	1	4	3
Summer 2022	6	1	0	1	4	5
Fall 2022	5	0	0	1	4	2
Winter 2022	1	0	0	0	0	1
Spring 2023	8	0	3	2	4	2
Summer 2023	8	0	0	3	4	1
Fall 2023	2	0	0	0	2	2

Table 5. Number of individual Paddlefish detected at each midstream Dannelly Reservoir backwater site for each season during the study period.

Midstream		Backwater Site				
Season	Numbers of Unique Individuals	4006	4007	4008	4009	4010
Winter 2021	3	1	0	1	2	0
Spring 2022	5	0	0	3	2	1
Summer 2022	0	0	0	0	0	0
Fall 2022	0	0	0	0	0	0
Winter 2022	1	0	0	1	0	0
Spring 2023	4	0	0	2	2	0
Summer 2023	0	0	0	0	0	0
Fall 2023	0	0	0	0	0	0

Table 6. The five most visited backwater sites throughout the study, seasons during which they were visited, and their general characteristics. n is the number of unique individuals that visited the site.

Receiver	Days	n	Section	Seasons	Characteristics
4004	513	7	Downstream	Spring - Fall	Relatively large, fed by Chilatchee Creek, narrow mouth, numerous Paddlefish observed breaching during spring and summer manual tracking
4003	277	4	Downstream	Spring - Fall	Mid-sized, full of submerged timber, wide and shallow mouth, numerous Paddlefish observed breaching during spring, summer, and fall manual tracking
4005	246	9	Downstream	All four	Medium-large, fed by Bogue Chitto Creek, narrow mouth with sections of narrow waters leading to larger waters
4008	45	5	Midstream	Winter & Spring	Mid-sized, fed by Big Swamp Creek, narrow and shallow mouth, full of flooded timber
4009	19	6	Midstream	Winter & Spring	Medium-small, fed by Cooks Creek, narrow and shallow mouth, full of flooded timber

Table 7. AIC table for GLMM evaluating factors associated with backwater use by Paddlefish in Dannelly Reservoir. Factors are daily and weekly percent change in gage height, depth, gage height, fish girth, length and weight, release location, fish sex, temperature and depth where the fish was detected, and zooplankton density. Degrees of freedom for each model, AIC score, change in AIC, and model weight are also included.

Intercept	Day chg.	Depth	Gage	Girth	Length	Rls.	Sex	Temp.	Wk. chg.	Weight	Zp.density	df	logLik	AIC	delta	wt.
1.9E-08	NA	0.45	1.14	0.00012	NA	NA	NA	94.68	0.51	14353.61	0.00039	9	-807.69	1633.39	0.00	0.10
0.00062	NA	0.45	1.14	0.00000	NA	+	+	94.59	0.51	1725750.66	0.0004	12	-804.81	1633.61	0.23	0.09
1.5E-07	NA	0.45	1.14	0.00003	NA	+	NA	94.62	0.51	105420.57	0.00039	10	-806.99	1633.98	0.59	0.07
9.9E-09	NA	0.45	1.14	NA	NA	NA	NA	94.27	0.51	NA	0.00039	7	-810.16	1634.33	0.94	0.06
1.3E-08	NA	0.45	1.14	NA	3.06	NA	NA	94.56	0.51	NA	0.00039	8	-809.63	1635.26	1.87	0.04
1.9E-08	0.98	0.45	1.14	0.00012	NA	NA	NA	95.42	0.51	14405.84	0.00039	10	-807.66	1635.33	1.94	0.04
1.9E-08	NA	0.45	1.14	0.00012	0.93	NA	NA	94.67	0.51	16546.00	0.00039	10	-807.69	1635.38	2.00	0.04

Table 8. Number of individual Paddlefish detected near potential spawning areas when temperatures were between 10-17C, the first and last dates for male and female fish to arrive, and the average minimum and maximum temperatures detected in these areas during spawning months (February - May).

Season 1 (2021-22)

Habitats	n	First Date (M)	First Date (F)	Last Date (M)	Last Date (F)	Min. Temp.	Max Temp.
R.F. Henry Tailrace	1	none detected	3/23/22	none detected	4/1/22	14.8	16.59
RKM 354-375 Gravel Beds	2	3/20/22	4/6/22	3/21/22	4/6/22	14	17.2
Cahaba River	2	none detected	2/5/22	none detected	4/20/22	13.2	16.4

Season 2 (2022-23)

Habitats	n	First Date (M)	First Date (F)	Last Date (M)	Last Date (F)	Min. Temp.	Max Temp.
R.F. Henry Tailrace	8	3/13/23	3/14/23	3/14/23	3/31/23	14.8	20.4
RKM 354-375 Gravel Beds	28	2/16/23	2/15/23	4/3/23	3/26/23	9.42	24.18
Cahaba River	4	2/1/23	none detected	2/22/23	none detected	11.47	18.8

Figures

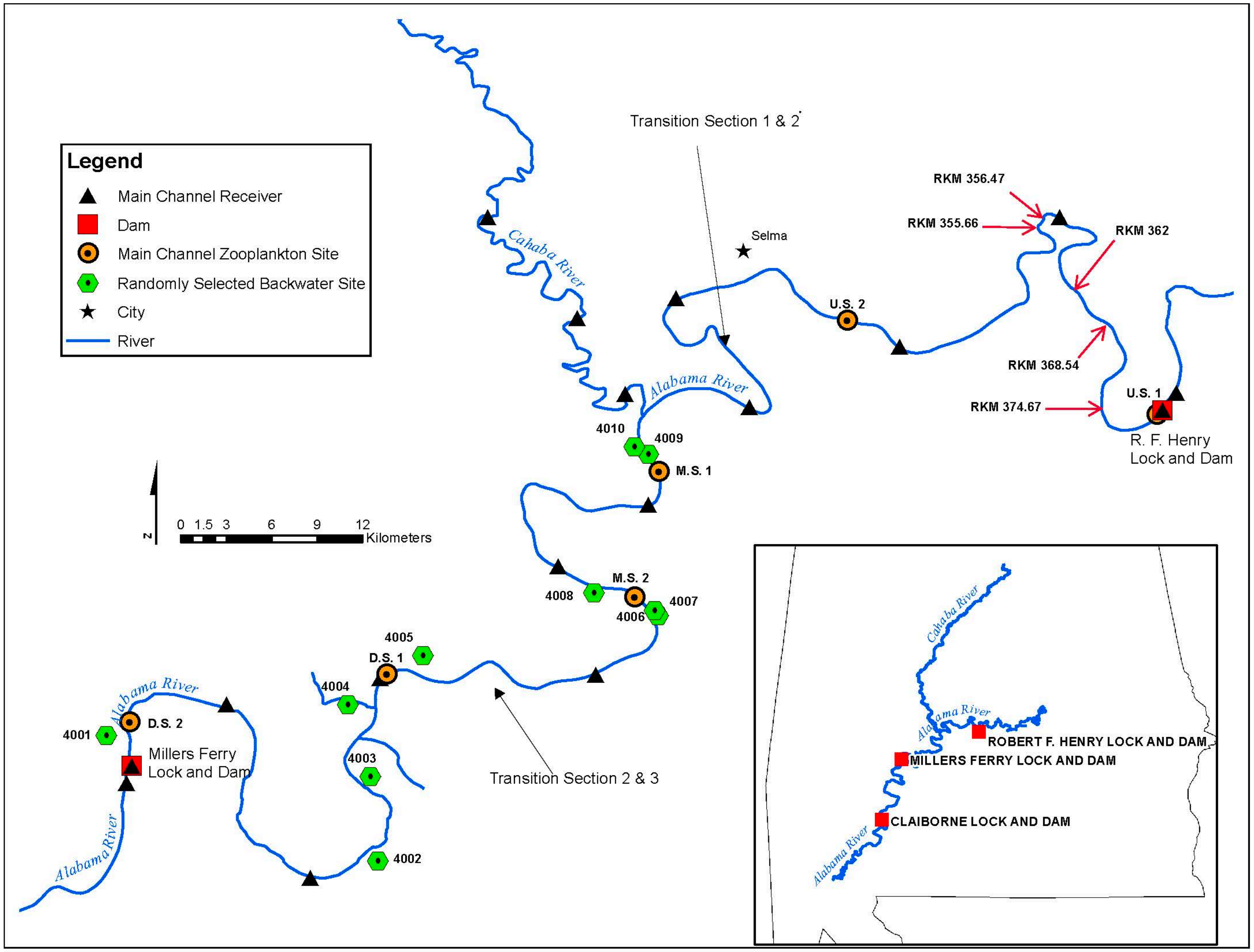

Figure 1. Map of the study area that includes section delineations, receiver locations and zooplankton sampling sites. Red arrows at the top indicate gravel beds identified during the study.

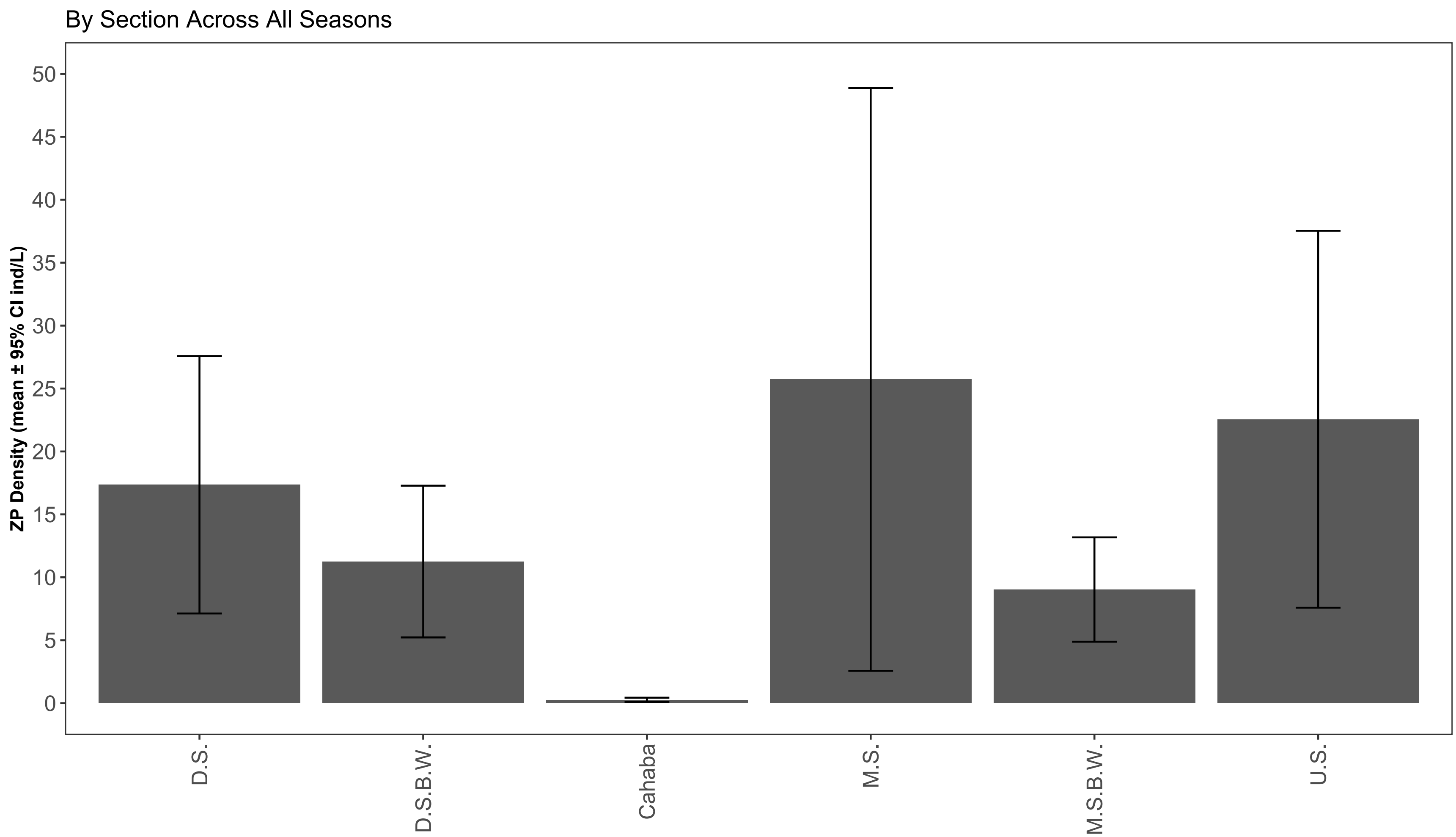

Figure 2. Zooplankton densities (mean ± 95% CI) in each river section when averaged across all seasons.

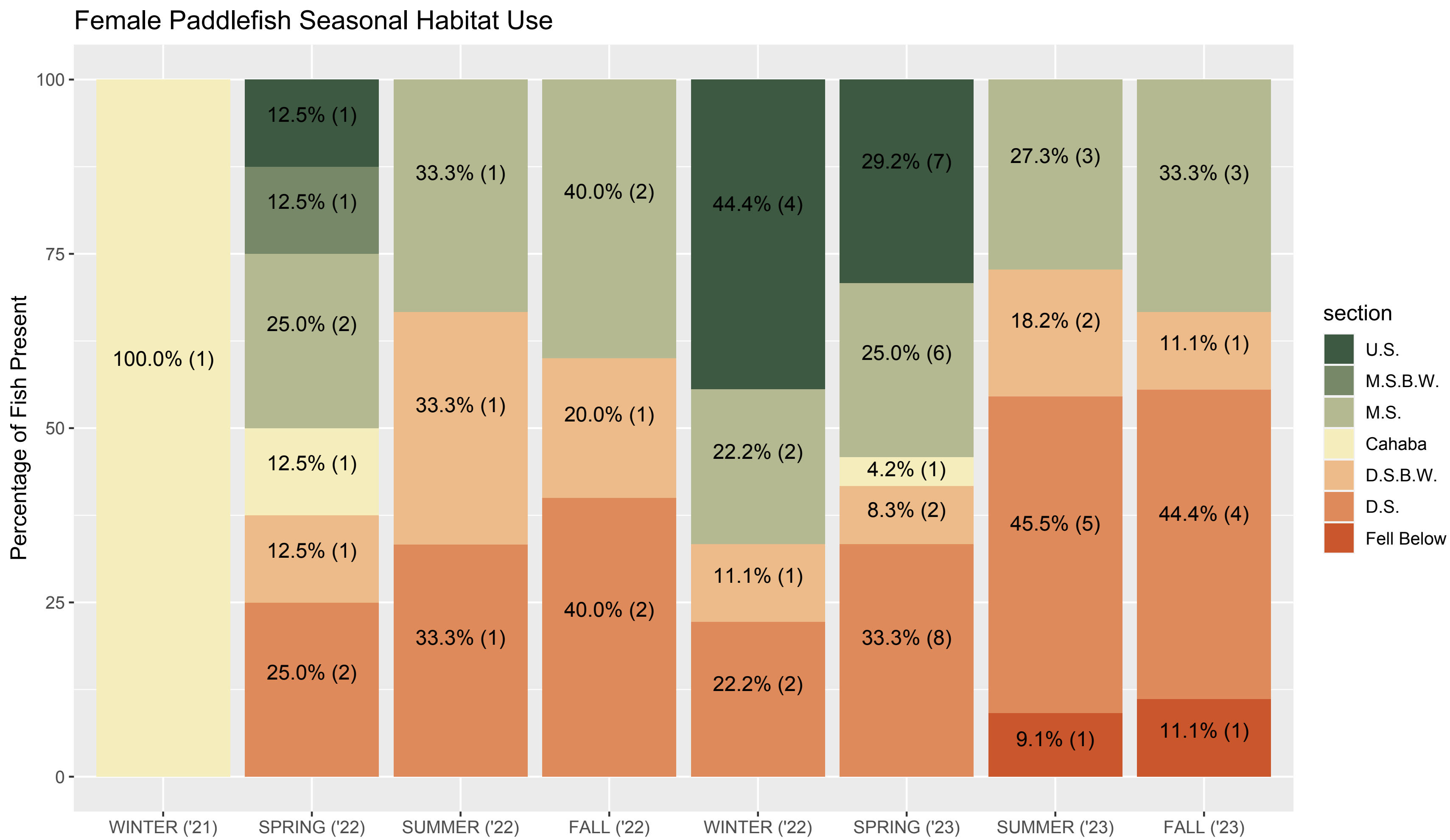

Figure 3. Percentage of female tagged fish found in each river section during each season and year.

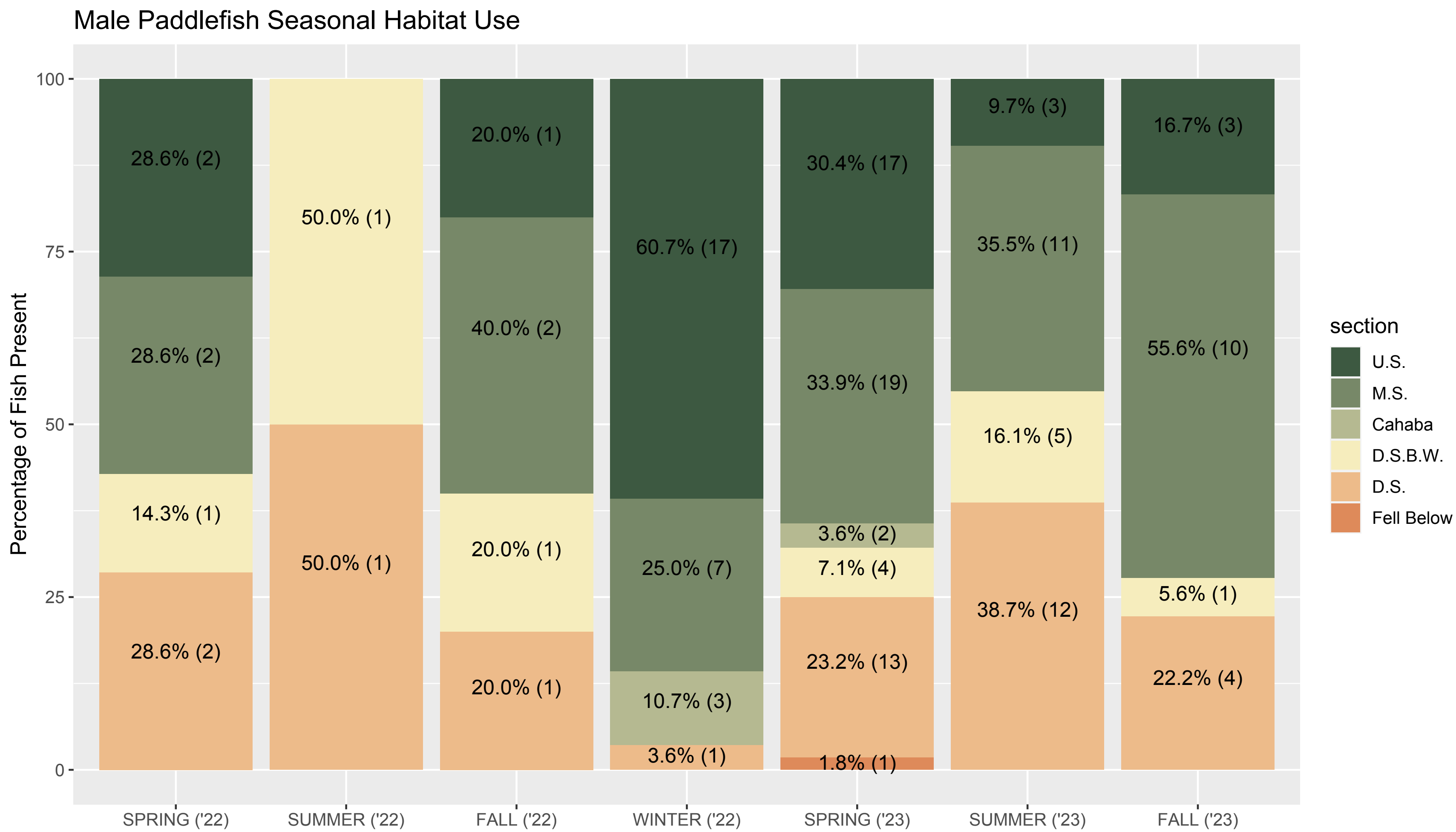

Figure 4. Percentage of male tagged fish found in each river section during each season and year.

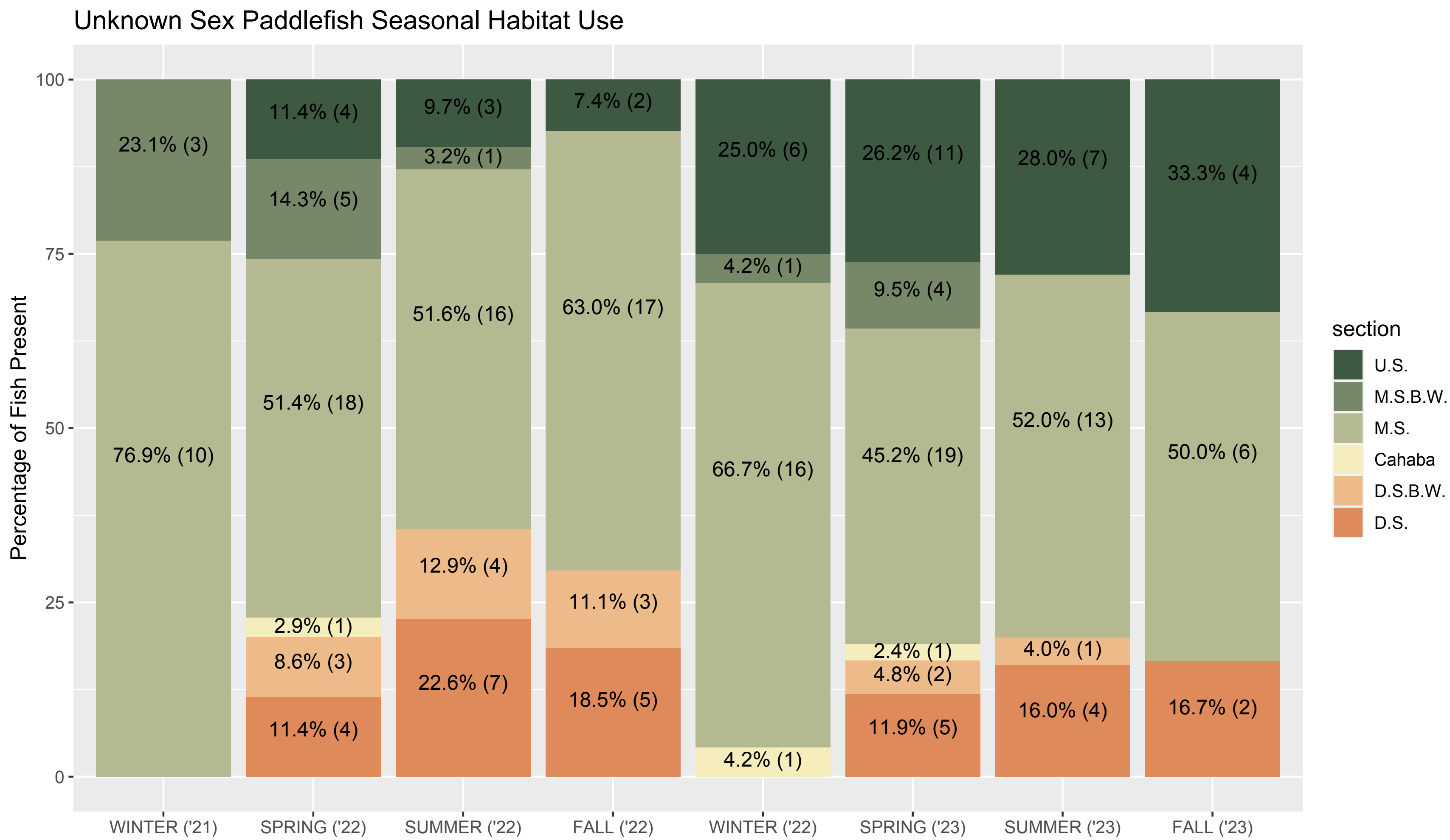

Figure 5. Percentage of unknown sex tagged fish found in each river section during each season and year.

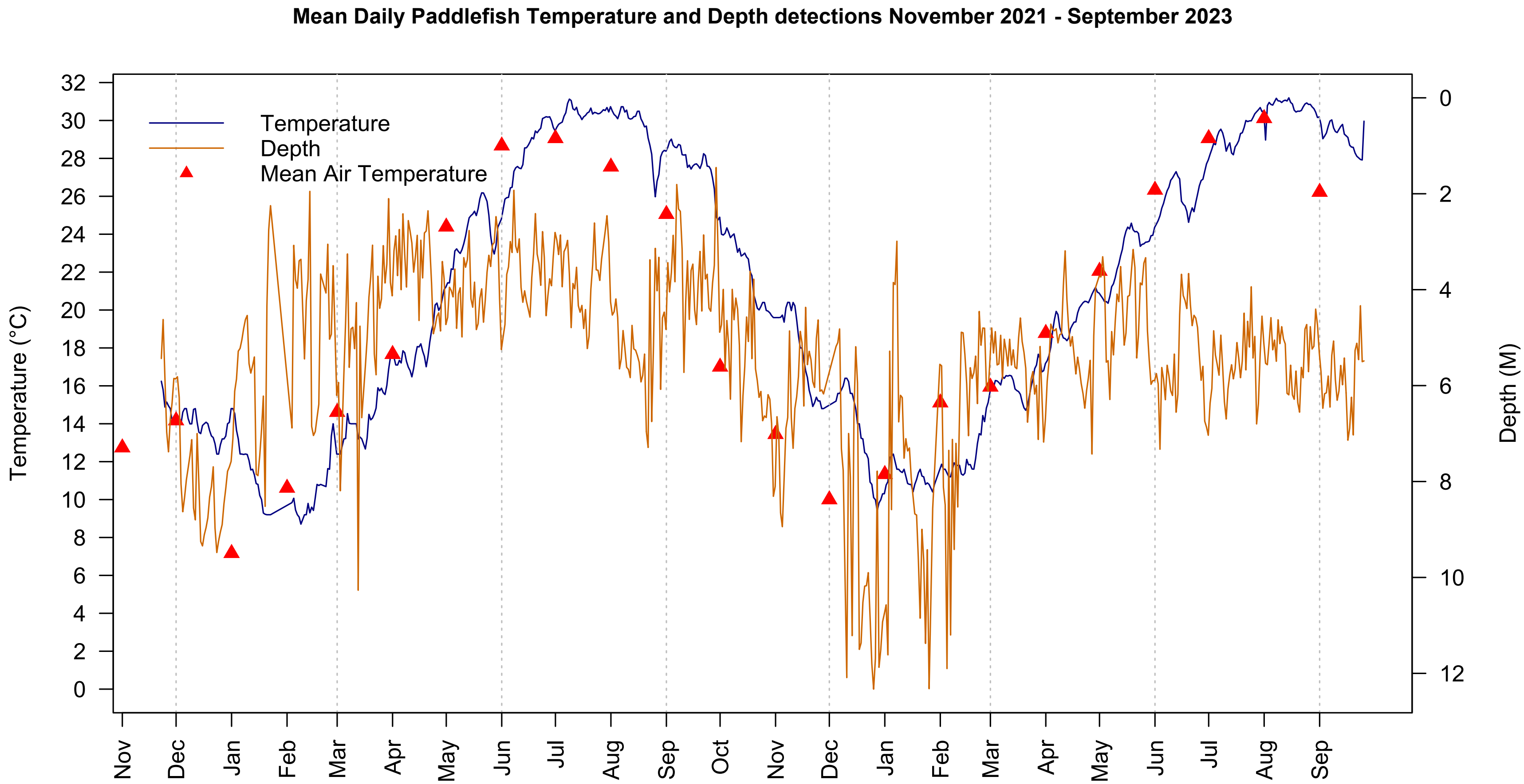

Figure 6. Average daily temperatures and depths transmitted from tagged fish, and average monthly air temperatures in Selma, AL.

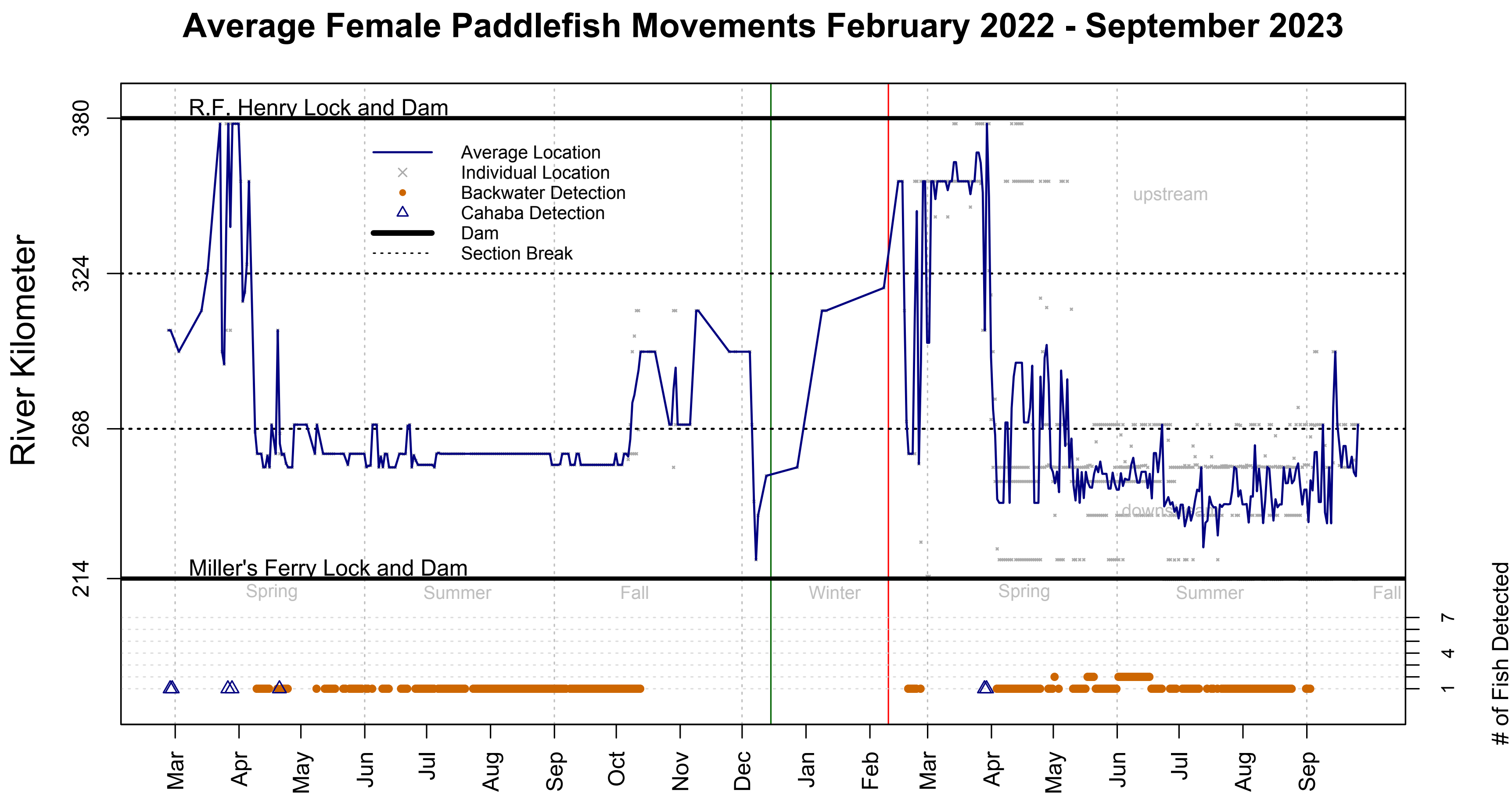

Figure 7. Average daily female Paddlefish location, average location for all females, backwater detections, Cahaba River detections, and numbers of fish detected. The vertical green line indicates the start of the 2022-23 tagging season. The vertical red line indicates when I began tagging fish in the upstream section.

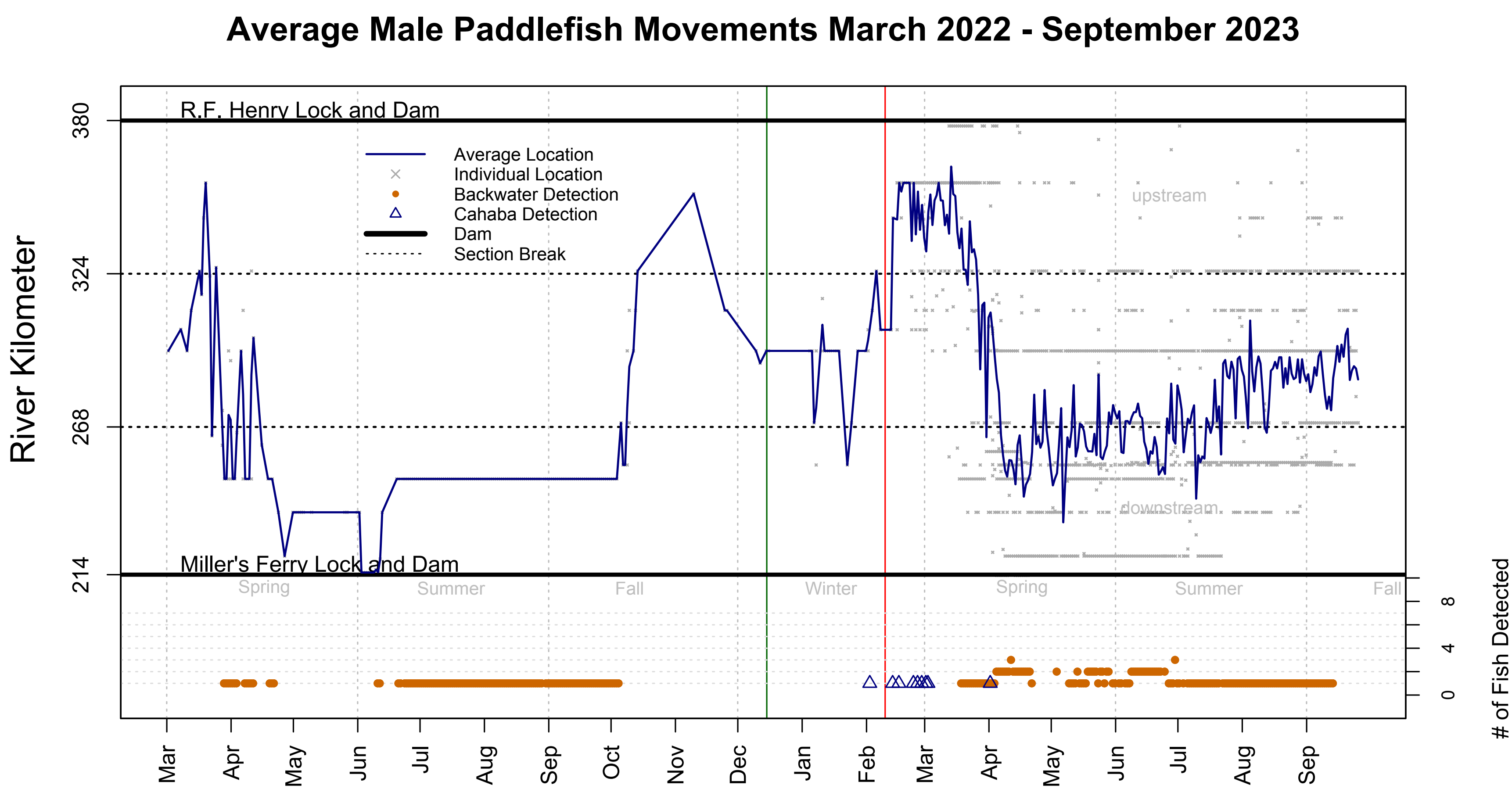

Figure 8. Average daily male Paddlefish location, average location for all females, backwater detections, Cahaba River detections, and numbers of fish detected. The vertical green line indicates the start of the 2022-23 tagging season. The vertical red line indicates when I began tagging fish in the upstream section.

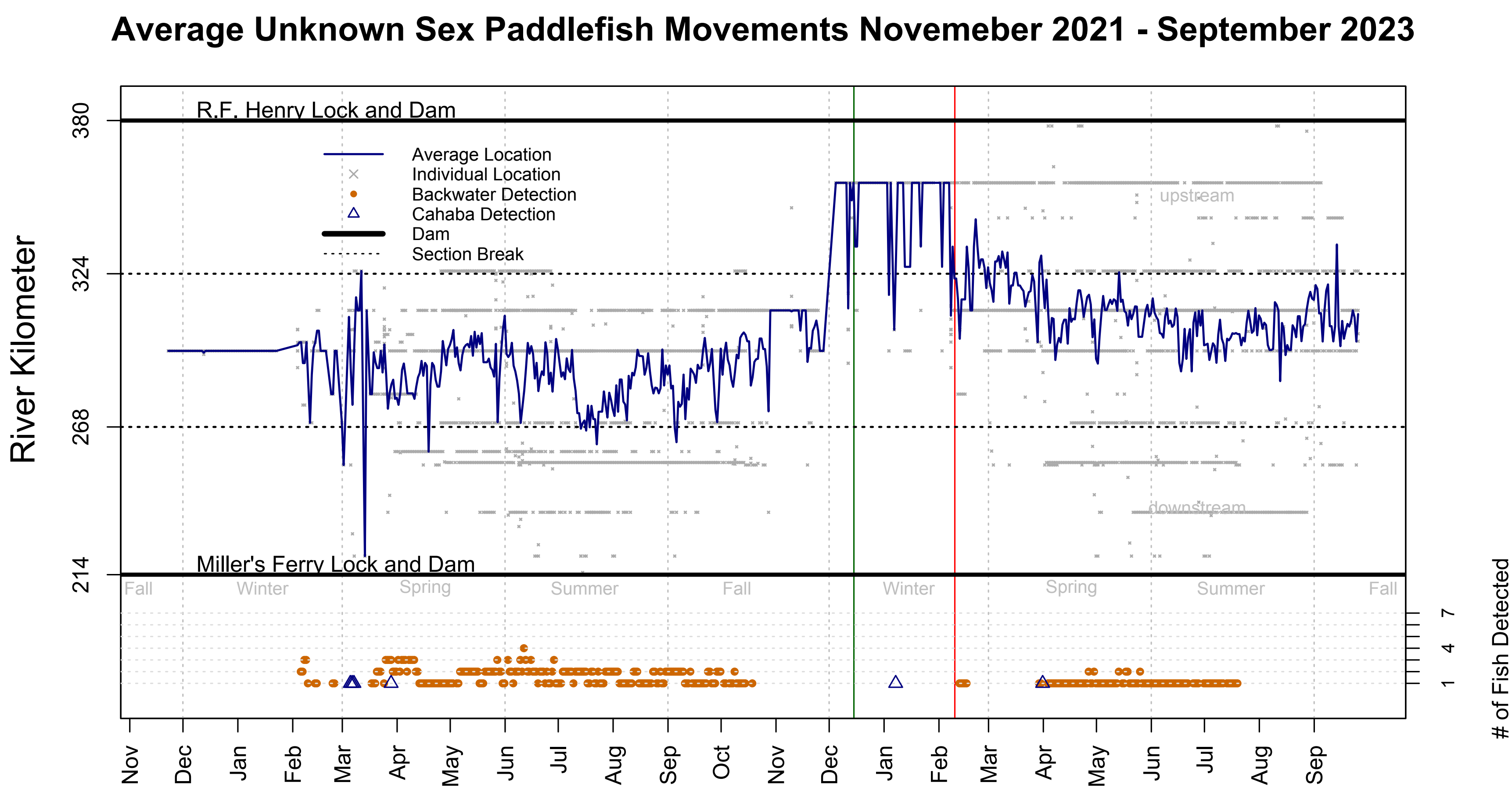

Figure 9. Average daily male Paddlefish location, average location for all females, backwater detections, Cahaba River detections, and numbers of fish detected. The vertical green line indicates the start of the 2022-23 tagging season. The vertical red line indicates when I began tagging fish in the upstream section.

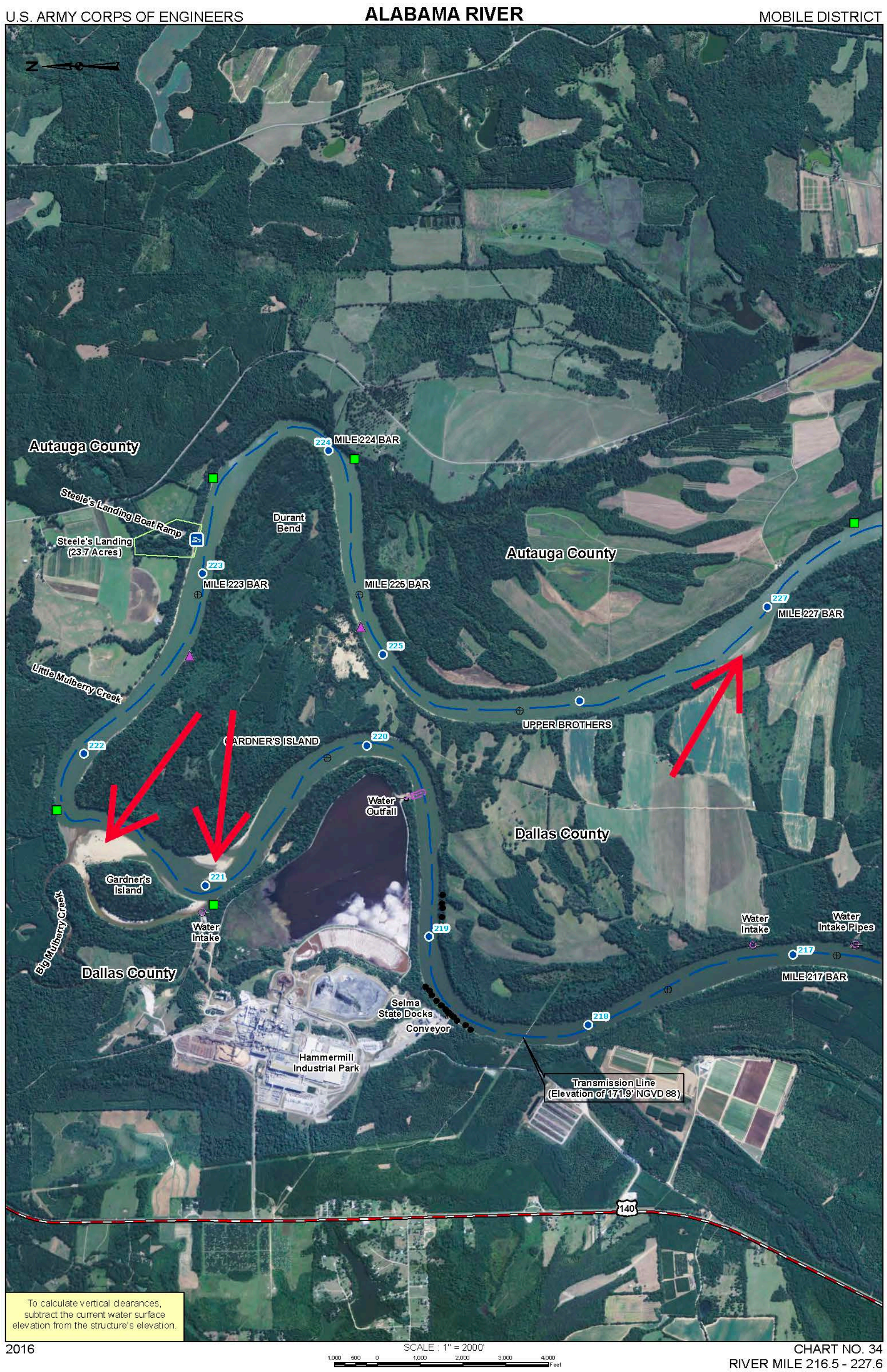

Figure 10. U.S. Army Corps of Engineers navigational chart with arrows indicating potential spawning habitat near RKM 355-362.

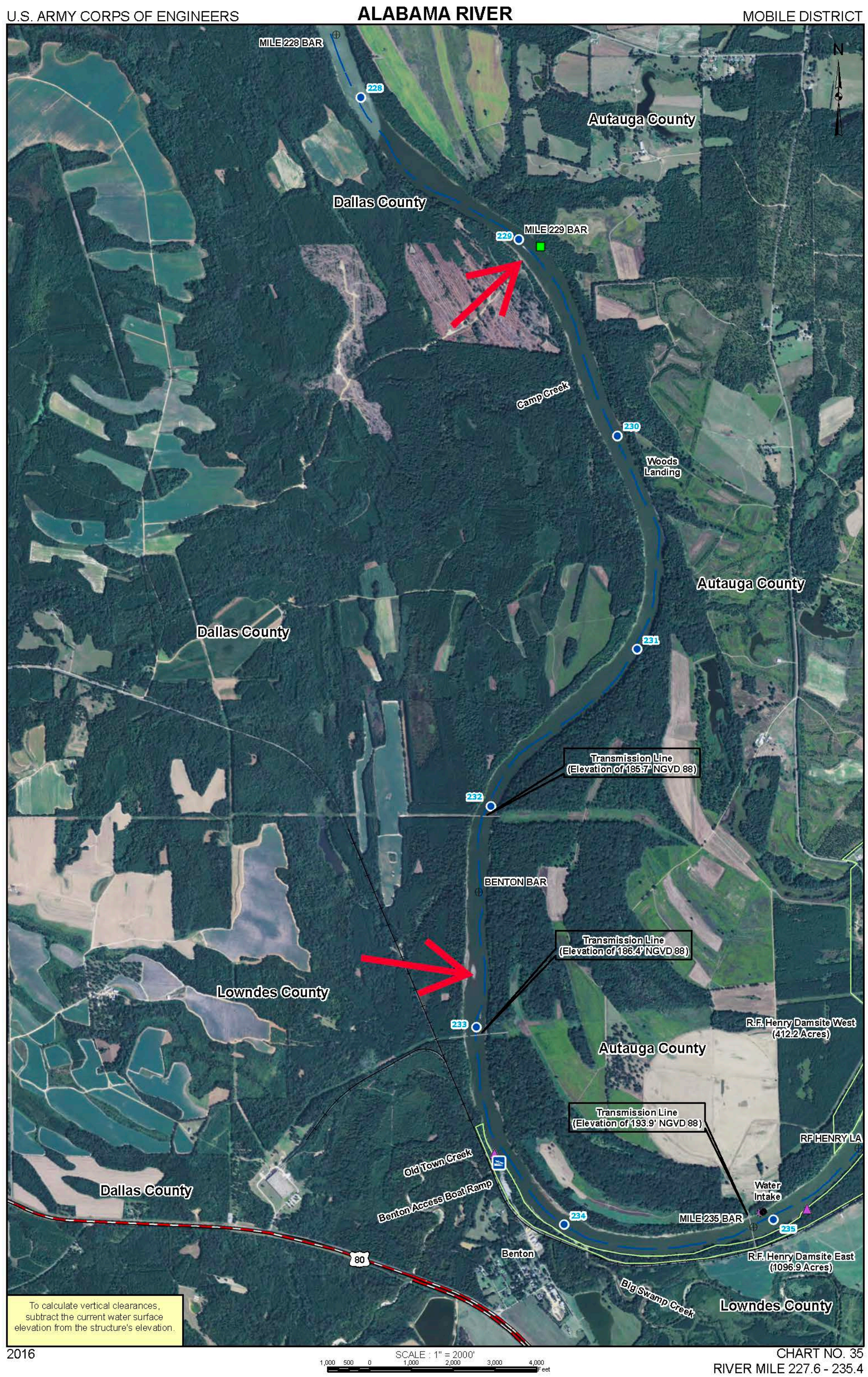

Figure 11. U.S. Army Corps of Engineers navigational chart with arrows indicating potential spawning habitat near RKM 368-375.

Appendix 1

Summary statistics for gage data by season and section.

		Gage Height				Daily % Change in Gage Height				Weekly % Change in Gage Height			
Section	Season	Mean	Min.	Max.	SD	Mean	Min.	Max.	SD	Mean	Min.	Max.	SD
Upstream	Fall	18.99	18.47	19.47	0.24	0.03	-3.36	2.74	1.11	1.83	-2.93	6.39	2.88
	Spring	22.67	18.07	41.28	4.49	-0.42	-22.29	46.79	9.37	-12.78	-44.79	18.58	18.27
	Summer	19.30	18.46	26.09	0.96	0.14	-18.70	29.36	3.52	0.93	-17.24	16.58	9.00
	Winter	24.90	18.99	34.53	4.14	-0.94	-12.37	37.48	9.23	0.65	-47.07	50.07	21.19
Midstream	Fall	18.96	17.68	22.35	0.42	0.01	-10.38	26.41	2.38	1.23	-2.93	32.68	3.61
	Spring	21.79	18.07	41.28	3.16	-1.36	-22.29	46.79	8.31	-7.52	-44.79	18.58	17.91
	Summer	19.36	18.46	26.09	0.94	0.17	-18.70	29.36	4.03	-0.03	-17.24	16.58	8.09
	Winter	25.08	19.35	34.96	4.29	0.63	-11.44	42.63	9.48	2.27	-47.07	50.07	23.38
Midstream Backwaters	Spring	31.49	19.41	41.28	6.39	1.50	-16.54	46.79	13.02	-21.89	-44.79	18.58	16.42
	Winter	32.18	21.62	41.40	7.57	1.86	-14.70	24.43	10.76	-7.05	-47.07	50.07	41.74
Cahaba	Spring	30.58	20.30	39.84	6.30	-1.17	-13.30	26.36	14.78	-17.20	-44.79	-1.70	8.50
	Winter	27.13	21.19	34.90	3.94	-1.73	-11.00	14.30	7.44	6.41	-11.72	50.07	24.40
Downstream	Fall	18.87	17.68	19.42	0.25	-0.02	-5.54	2.16	1.14	1.48	-2.93	6.39	2.07
	Spring	21.70	18.07	39.84	2.54	-0.80	-22.29	26.36	6.62	-4.48	-44.79	18.58	17.90
	Summer	19.57	18.46	26.09	1.41	0.36	-18.70	29.36	5.43	0.29	-17.24	16.58	7.94
	Winter	24.28	19.12	34.90	4.66	1.35	-8.36	16.78	7.59	5.24	-11.72	22.39	13.56
Downstream Backwaters	Fall	18.98	17.68	22.35	0.84	-0.08	-10.38	26.41	4.62	1.33	-2.93	6.39	2.83
	Spring	22.52	18.07	41.28	4.31	-0.16	-22.29	46.79	8.39	-6.25	-44.79	18.58	19.81
	Summer	19.55	18.46	26.09	1.35	0.03	-18.70	29.36	5.07	0.44	-17.24	16.58	7.89
	Winter	28.21	24.03	34.53	4.52	-3.30	-11.00	7.07	5.58	-10.64	-10.64	-10.64	0.00

Appendix 2

Summary statistics for fish body metrics at the time of tagging by season and section where they were detected.

		Fish Weight				Fish Length				Fish Girth			
Section	Season	Mean	Min.	Max.	SD	Mean	Min.	Max.	SD	Mean	Min.	Max.	SD
Upstream	Fall	6.82	3.77	9.29	1.48	806.71	655.00	932.00	73.58	435.83	345.00	504.00	45.76
	Spring	8.42	3.65	14.42	2.27	861.25	655.00	975.00	67.37	472.95	342.00	615.00	60.24
	Summer	7.10	3.77	8.95	1.58	825.40	655.00	919.00	73.06	447.30	345.00	516.00	52.35
	Winter	7.87	3.65	12.65	1.78	855.26	686.00	946.00	47.99	466.99	342.00	590.00	42.73
Midstream	Fall	7.33	4.18	12.65	1.84	833.16	724.00	946.00	62.55	451.46	382.00	590.00	44.99
	Spring	7.57	3.65	14.42	2.08	837.45	655.00	975.00	70.55	453.59	342.00	615.00	50.13
	Summer	7.10	3.77	12.65	1.68	824.35	655.00	926.00	65.01	445.14	345.00	590.00	41.90
	Winter	7.60	3.77	14.48	1.88	852.73	655.00	1001.00	57.30	450.27	345.00	612.00	49.43
Midstream Backwaters	Spring	7.52	3.65	9.54	1.67	871.64	686.00	926.00	58.64	448.48	342.00	516.00	53.63
	Winter	6.44	5.78	7.51	0.86	842.19	816.00	877.00	29.40	404.81	383.00	432.00	21.93
Cahaba	Spring	7.88	5.65	9.33	1.10	852.14	724.00	914.00	47.56	461.19	417.00	514.00	43.99
	Winter	7.51	5.65	9.33	1.70	828.60	724.00	932.00	91.95	451.90	417.00	514.00	40.88
Downstream	Fall	8.23	3.65	12.65	2.45	845.58	686.00	946.00	62.44	469.43	342.00	590.00	67.58
	Spring	9.38	3.65	14.48	2.32	876.62	686.00	1001.00	54.28	491.22	342.00	615.00	66.16
	Summer	9.18	3.65	14.42	2.71	855.52	686.00	975.00	61.22	494.47	342.00	615.00	74.66
	Winter	10.90	8.61	14.48	2.66	932.78	881.00	1001.00	52.13	529.83	454.00	612.00	65.41
Downstream Backwaters	Fall	7.97	5.46	12.65	1.49	859.67	747.00	932.00	50.21	458.20	383.00	590.00	41.21
	Spring	8.87	3.65	12.65	2.13	880.01	686.00	944.00	52.21	469.95	342.00	590.00	56.90
	Summer	9.16	5.46	12.65	2.44	873.63	747.00	944.00	50.92	485.80	383.00	590.00	68.59
	Winter	14.48	14.48	14.48	0.00	1001.00	1001.00	1001.00	0.00	612.00	612.00	612.00	0.00

Appendix 3

Summary statistics for zooplankton density, temperatures and depth by season and section where fish were detected.

		Zooplankton Density				Temperature				Depth			
Section	Season	Mean	Min.	Max.	SD	Mean	Min.	Max.	SD	Mean	Min.	Max.	SD
Upstream	Fall	36.08	26.41	54.14	5.90	28.41	22.80	30.00	2.00	5.78	1.39	11.35	1.91
	Spring	2.54	0.45	3.15	0.78	18.32	13.20	25.77	2.96	4.93	0.08	15.63	2.30
	Summer	32.71	18.96	38.89	8.73	27.90	23.31	30.94	2.09	4.82	0.02	15.12	2.90
	Winter	0.89	0.58	0.92	0.10	12.76	9.42	16.40	1.59	8.21	2.10	14.62	3.14
Midstream	Fall	29.94	17.60	67.25	20.05	25.58	14.75	32.08	4.26	6.02	0.01	14.30	2.67
	Spring	4.40	0.22	6.08	2.62	19.74	12.40	26.00	3.01	5.27	0.01	19.60	2.77
	Summer	76.77	2.75	185.16	78.49	28.64	23.91	33.20	2.05	5.72	0.02	20.06	2.89
	Winter	0.57	0.20	1.45	0.24	12.26	9.15	16.40	1.84	5.76	1.40	11.20	2.17
Midstream Backwaters	Spring	1.35	0.53	2.81	0.45	16.66	11.60	24.40	2.02	2.72	0.10	4.88	1.22
	Winter	1.62	0.75	4.86	1.15	9.95	8.74	11.60	0.95	2.38	0.10	4.85	1.65
Cahaba	Spring	0.55	0.07	0.85	0.38	16.67	13.20	18.80	1.61	4.12	1.72	14.66	3.68
	Winter	0.10	0.05	0.27	0.09	14.40	11.60	18.00	2.33	2.69	1.57	4.20	0.99
Downstream	Fall	20.21	16.05	30.94	6.70	27.40	16.40	30.70	3.25	6.12	0.86	16.10	2.68
	Spring	5.01	0.65	5.86	1.80	20.30	12.40	26.40	2.57	5.36	0.10	15.67	2.89
	Summer	31.92	22.93	69.77	17.62	28.32	22.80	31.60	2.10	5.43	0.10	13.65	2.89
	Winter	1.15	0.84	2.89	0.75	13.46	9.20	15.60	2.31	3.66	0.10	9.04	2.74
Downstream Backwaters	Fall	15.50	4.95	24.05	7.12	26.58	20.01	30.41	2.70	1.54	0.09	10.63	1.66
	Spring	2.03	0.31	6.97	1.81	22.01	13.87	28.39	3.16	2.12	0.01	9.25	1.82
	Summer	13.61	3.09	69.77	10.51	29.33	22.16	33.20	1.97	2.53	0.01	11.31	2.54
	Winter	0.66	0.66	0.66	0.00	15.07	11.60	18.00	2.63	1.79	0.32	3.42	0.81

Appendix 4

Pearson's correlation matrix for numeric response variables used in the GLMMs.

	Zooplankton density	Gage	% Daily Change	% Weekly Change	Temperature	Depth	Length	Girth	Weight
Zooplankton density	1.00	-0.22	0.04	0.12	0.42	0.05	-0.16	-0.17	-0.22
Gage	-0.22	1.00	0.12	-0.32	-0.59	-0.01	0.12	0.01	0.05
% Daily Change	0.04	0.12	1.00	0.17	0.09	-0.05	-0.04	0.00	-0.01
% Weekly Change	0.12	-0.32	0.17	1.00	0.39	-0.05	-0.06	-0.03	-0.05
Temperature	0.42	-0.59	0.09	0.39	1.00	-0.06	-0.13	0.02	-0.02
Depth	0.05	-0.01	-0.05	-0.05	-0.06	1.00	0.02	0.10	0.05
Length	-0.16	0.12	-0.04	-0.06	-0.13	0.02	1.00	0.73	0.82
Girth	-0.17	0.01	0.00	-0.03	0.02	0.10	0.73	1.00	0.96
Weight	-0.22	0.05	-0.01	-0.05	-0.02	0.05	0.82	0.96	1.00