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Movement, Habitat Use, Reproduction, and Commercial Harvest of Paddlefish in Lake Dardanelle, Arkansas

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MOVEMENT, HABITAT USE, REPRODUCTION, AND COMMERCIAL HARVEST OF PADDLEFISH IN LAKE DARDANELLE, ARKANSAS

By

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MOVEMENT, HABITAT USE, REPRODUCTION, AND COMMERCIAL HARVEST OF PADDLEFISH IN LAKE DARDANELLE, ARKANSAS

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THESIS ABSTRACT

Paddlefish *Polyodon spathula* are a valuable commercial species throughout much of their range including Lake Dardanelle, one of the most important commercial paddlefish fisheries in Arkansas. While fecundity, mortality, and age and growth of paddlefish stocks in Lake Dardanelle have been assessed previously, information on their movements, habitat utilization, and commercial harvest rates is lacking. To help fill this information gap, 39 paddlefish were tracked a minimum of once per month from October 2014 through September 2015. Habitat selection was determined for eight macrohabitat types and four bathymetric habitat types by comparing percent usage to percent availability. Four high-use (≥10%) and four moderate-use (4-10%) areas were identified. Paddlefish preferred deep pools and bays with relatively large tributaries. Median linear range was 1.9, 20.9, 1.2, and 9.7 km in winter, spring, summer, and fall, respectively. All seasonal differences were significant (all $P < 0.020$) except winter and summer ($P = 0.486$). As many as 14 individuals may have emigrated during a major flood event in the summer of 2015. Downstream emigration was confirmed for two individuals that were detected below Dardanelle Dam. Spawning runs were observed for nine paddlefish that likely spawned below Ozark Jeta-Taylor Dam when water temperatures were between 10 and 18 ^{o}C. Commercial fishing mortality on telemetered fish was 13% during the 2014-15 and 2015-16 commercial paddlefish seasons combined. Knowledge gained from this study will help managers maintain a viable and commercially productive paddlefish population in Lake Dardanelle.

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INTRODUCTION

Paddlefish *Polyodon spathula* are large, riverine fish that inhabit the medium and large rivers of the Mississippi River and Gulf Coast drainages in the central United States (Burr 1980, Carlson and Bonislawsky 1981). They are important both as a commercial species (Quinn 2009) and as a recreational species (Scarnecchia et al. 2007), and are managed as such throughout their range. Stocks declined in the late twentieth century, but are generally stable now as a result of increased management and research actions (Bettoli et al. 2009). Like acipenseriformes around the world, paddlefish are susceptible to overfishing, habitat alteration, and pollution (Gerken and Paukert 2009). The International Union for the Conservation of Nature lists them as "vulnerable" on the Red List of Threatened Species.

Taxomony. Paddlefish have existed on earth for approximately 135 million years (Grande et al. 2002). Once considered to be freshwater sharks, they are now in the order Acipenseriformes, which contains the sturgeons and paddlefishes (Kuhajda 2014). They are one of only two extant species in the family Polyodontidae, although the other species, the Chinese paddlefish *Psephurus gladius*, is near extinction (Zhang et al. 2009). While *P. spathula* are sometimes thought of as primitive, they are actually highly derived, as evidenced by the fossil record (Grande and Bemis 1991). *Polyodon spathula* and the extinct *Polyodon tuberculata*, the two known species in the genus *Polyodon*, share adaptive traits such as long gill rakers and an elongated lower jaw that are absent in the more primitive paddlefishes (Grande and Bemis 1991; Kuhajda 2014).

Biology and physiology. Paddlefish have a unique morphology that is well suited to the riverine environment in which they evolved. They commonly grow to large sizes

and have been reported up to 72 kg (Epifanio et al. 1996). Easily distinguished by a prominent rostrum, paddlefish also have a large mouth, a heterocercal tail, and lack scales, with the exception of three vestigial denticular scales found near the caudal peduncle (Kuhajda 2014).

Paddlefish feed by ram filtering; the mouth is held agape and food items are collected in numerous gill rakers as water moves across them (Sanderson et al. 1994). Zooplankton larger than 100 µ make up the majority of paddlefish diet (Rosen and Hales 1981), but Hoopes (1960) noted that mayflies can also be a significant source of food. While feeding, paddlefish use a remarkable electrosensory system to locate and target prey items (Wilkens and Hoffman 2007). Numerous ampullae of Lorenzini that cover the rostrum, head, and opercular flaps are able to detect the electrical fields produced by zooplankton (Russell et al. 1999; Wilkens and Hoffman 2007).

Paddlefish are obligate ram ventilators and lack the ability to pump water over their gills efficiently (Burggren and Bemis 1991). Thus, they must move continuously through the water or hold position in current to maintain respiration. A fusiform body shape and narrow caudal fin, which reduce drag, and a wide rostrum which generates lift, facilitate respiration by lowering the metabolic costs of continuous movement (Kuhajda 2014).

Movement. Numerous studies have shown that paddlefish are capable of moving long distances, both upstream and downstream, even when dams are present (Rosen et al. 1982; Southall and Hubert 1984; Moen et al. 1992; Stancill et al. 2002; Zigler et al. 2004; Donabauer et al. 2009; Mettee et al. 2009; Pracheil 2012). Most large-scale movements are associated with spring spawning migrations, when paddlefish move upstream

(Rehwinkel 1978; Southall and Hubert 1984; Firehammer and Scarnecchia 2006a; Donabauer 2007). Once paddlefish reach a general spawning area, the direction of their movements is correlated with flow levels. During higher flows they move upstream, and during lower flows they retreat to downstream staging areas (Firehammer and Scarnecchia 2006b). However, the longest recorded paddlefish movements were not associated with spawning. Rosen et al. (1982) reported that one individual moved nearly 2,000 km downstream, and Stancill et al. (2002) reported that another individual moved 1,900 km downstream through five dams.

The presence of numerous dams in historically unimpeded rivers may reduce gene flow and overall species fitness by partially blocking movements (Stancill et al. 2002). While paddlefish can clearly pass through dams at times (Moen at al. 1992; Mettee et al. 2009), the efficiency with which they do so is influenced by water levels (Zigler et al. 2004). Thus, paddlefish attempting to move long distances may be dependent on major flood events.

Life history. Paddlefish eggs are oval, black or gray, range in diameter from 2.0 to 4.0 mm, and become adhesive once they are fertilized (Purkett 1961; Ballard and Needham 1964; Rosen 1976). Purkett reported that hatching began 6-7 d after fertilization at water temperatures 18-21ºC, but lower water temperatures increase the amount of time that eggs take to hatch (Ballard and Needham 1964; Jennings and Zigler 2009). Larval paddlefish are approximately 8.8 mm when they first emerge from the egg, and immediately swim upward in the water column so that they may catch the current and drift passively (Purkett 1961). Paddlefish larvae are capable swimmers by time they reach 13.1 mm in length (Adams et al. 1999), and begin actively feeding on zooplankton

at 15.0 mm (Ballard and Needham 1964; Ruelle and Hudson 1977). Juvenile paddlefish morphology is similar to that of adults, except that the rostrum is larger in proportion to the body in juveniles because rostrum growth is negatively allometric (Hoover et al. 2000).

The age at which paddlefish become sexually mature varies regionally. Males become mature at ages 5-7 in most populations (Reed et al. 1992; Hoffnagle and Timmons 1989; Lein and Devries 1998; Timmons and Hughbanks 2000; Scarnecchia et al. 2011), but do not mature until ages 8-12 in northern populations in Montana and North Dakota (Scarnecchia et al. 2007). Females become mature at ages 5-6 in Alabama (Lein and Devries 1998); at ages 8-9 in Arkansas, Kentucky, Louisiana, Oklahoma, and Tennessee (Hoffnagle and Timmons 1989; Reed et al. 1992; Lein and Devries 1998; Timmons and Hughbanks 2000; Scarnecchia 2011; Leone et al. 2012); and at ages 15-19 in Montana and North Dakota (Scarnecchia 2007). While males are capable of spawning every year, females in most populations probably only spawn once every 2-5 years (Carlson and Bonislawsky 1981; Lein and DeVries 1998; Jennings and Zigler 2000). However, Sharov et al. (2014) contended that conclusions on female spawning periodicity have been drawn from a small number of studies that rely on indirect evidence, and that female spawning frequency may not be fully explained by the current model.

Paddlefish move upstream to spawn in the spring when water temperatures are 10-21 ^{o}C (Purkett 1961; Lein and DeVries 1998; O’Keefe 2007; Donabauer et al. 2009). Broadcast spawning is triggered by increased flows, and occurs over gravel, sand, and bedrock substrates (Purkett 1961; Firehammer et al. 2006; O’Keefe 2007). Purkett

(1961) observed spawning in the Osage River, Missouri, and suggested that a spawning aggregation, consisting of a single female and multiple males, release gametes while making their way from deep in the water column to the water's surface. The activity is apparently repeated multiple times.

Habitat use. Paddlefish habitat use varies among regions and seasons. Historically, paddlefish used the deeper, slower areas of oxbow lakes and side channels found in large rivers (Stockard 1907). In the few remaining unaltered rivers within their range, paddlefish mostly use low current velocities in deep scour holes immediately downstream of sandbars, but occasionally use backwaters as well (Rosen et al. 1982). Most present-day paddlefish rivers, however, are profuse with dams, dikes, and fortified banks. In these refashioned rivers, paddlefish often use tailwaters, navigation structures, and tributary mouths where deep water and slow current velocities can be found (Southall and Hubert 1984; Moen et al. 1992; Zigler et al. 2003; Donabauer 2007). Backwaters and shallow areas are typically avoided (Southall and Hubert 1984; Moen et al. 1992; Zigler et al. 2003), but not always (Clark-Kolaks et al. 2009). In all waters, altered or unaltered, paddlefish congregate in the deepest pools available during winter (Rosen 1982; Paukert and Fisher 2001a; Stancill et al. 2002). Notably, paddlefish use of aquatic area types varies considerably, depending on the study area. For example, Zigler et al. (2003) reported that impounded areas were preferred in Pool 5 of the Mississippi River, but avoided in Pool 8. Differences across studies in aquatic area type use, but not in depth or current velocity use, suggest that depth and current velocity, rather than aquatic area type, are the most important factors in assessing why paddlefish select certain areas over others (Zigler et al. 2003).

Harvest. Paddlefish have been harvested for centuries in North America. Native American rock art in Petit Jean State Park, Arkansas that depicts a paddlefish and a woven fish trap dates to over 500 years old (Berg-Vogel 2005). Paddlefish were primarily targeted for their flesh until the late nineteenth century, when a collapse in overfished sturgeon stocks and a high demand for caviar caused commercial fisherman to begin targeting paddlefish for their roe (Scholten 2009). While fishing pressure fluctuated in the 1900s, overfishing eventually lead to the depletion of many paddlefish stocks throughout their range (Stockard 1907; Alexander 1914; Pasch and Alexander 1986). Concerns about overfishing prompted several states to completely close commercial fishing as early as the 1970s (Scholten 2009), and currently only eight states allow commercial fishing (Alabama, Arkansas, Illinois, Indiana, Kentucky, Mississippi, Missouri, and Tennessee).

Paddlefish are also harvested recreationally; typically they are taken by snagging, but archery is also used (Quinn 2009). The recreational harvest of paddlefish is currently allowed in eleven states, but regulations vary among states. For example, Arkansas allows the harvest of two paddlefish per person per day for the entire year, while Montana allows the harvest of one paddlefish per person per year, and paddlefish fishing is halted once a statewide quota is reached. Recreational fishers in North America generally do not keep paddlefish eggs (Scarnecchia et al. 1996). This lack of utilization prompted two state agencies (Montana Fish, Wildlife, & Parks and the Oklahoma Department of Wildlife Conservation) to establish operations that offer paddlefish fillet processing to recreational fishers in exchange for roe, which is then sold as caviar. Profits from the operations are used to fund management and research activities.

CHAPTER I

INTRODUCTION

Paddlefish in Arkansas are found in major rivers and their larger tributaries including the Mississippi, Arkansas, White, Red, and Ouachita rivers (Robison and Buchanan 1988). They are routinely sampled by fisheries agencies, and specific evaluations over a wide range of topics have been conducted within the state over the last decade. Statewide populations are thought to be stable (Jennings and Zigler 2009), but stocks in the Arkansas River may be overfished (Sharov et al. 2014).

In Arkansas, paddlefish are primarily important as a commercial species, and are mostly pursued for their valuable roe. The Arkansas River was third in roe harvest during the 2007-08 commercial season behind the Mississippi and White rivers (Posey 2008). A marked decrease in roe harvest from Lake Dardanelle and Ozark Lake after 2006 indicated that overfishing may have occurred (Posey 2008). Currently, commercial fishing on Lake Dardanelle is restricted to a 151 d commercial season each year; seasons begin on November 20 and close on April 10 of the following year. Recreational snagging is allowed year-round on Lake Dardanelle, but only within 91 m below a dam. This effectively limits harvest by snag fishermen to spring spawning runs.

Several studies have examined the biology and life history of paddlefish in the Arkansas River (Paukert and Fisher 2000; Paukert and Fisher 2001a; Paukert and Fisher 2001b; Donabauer et al. 2009; Leone et al. 2012). Paukert and Fisher (2000, 2001a) found that paddlefish movements in Keystone Reservoir, Oklahoma during spring and summer were influenced by water level as well as physiochemical conditions, and suggested that paddlefish successfully spawn throughout the reservoir system.

Donabauer et al. (2009) telemetered paddlefish in Pool 13 and Ozark Lake, Arkansas, and reported that paddlefish selected different habitats in each pool. Donabauer (2007) also observed upstream spawning migrations and confirmed successful reproduction below James W. Trimble Dam. Leone et al. (2012) assessed population characteristics in Pool 13, Ozark Lake, and Lake Dardanelle, Arkansas, and found that fish in Lake Dardanelle had higher fecundity, condition, and mortality than those in Pool 13 and Ozark Lake. However, investigations into movements, habitat utilization, and commercial harvest have not been conducted on Lake Dardanelle, even though it remains an important commercial fishery.

The main goal of my study was to increase knowledge of paddlefish biology for the purpose of enhancing managers' abilities to survey populations, regulate harvest rates, and monitor habitat. The primary objectives of this study were to: (1) determine paddlefish movement and habitat use; (2) identify paddlefish spawning locations; and (3) estimate fishing mortality of paddlefish.

METHODS

Study area. The Arkansas River is the sixteenth largest river in the United States in terms of discharge (USGS 1990), and the second largest western tributary of the Mississippi River (Hocutt and Wiley 1986). It flows 2,400 km from its source in the Rocky Mountains of Colorado to its confluence with the Mississippi River on the border of Arkansas and Mississippi. The entire watershed drains 417,000 km^2 (USGS 1990). The McClellan-Kerr Arkansas River Navigation System (MKARNS) was completed in 1971, and is made up of a series of 18 locks and dams, numerous wing dikes, and rip rap fortified banks, which are distributed over the lower 700 river km of the river. It provides

commercial navigation, bank stabilization, flood control, and hydroelectric power generation (Limbird 1993).

Lake Dardanelle (Pool 10) is approximately 16,200 ha and is delineated by Dardanelle Lock and Dam 10 on the downstream end and Ozark-Jeta Taylor Lock and Dam 12 on the upstream end (Figure 1.1). Lock and Dam 11 would have been located in the middle of Lake Dardanelle but was never constructed. The distance from Dardanelle Lock and Dam to Ozark-Jeta Taylor Lock and Dam is approximately 82.6 river km (USACE 2014). For my study Lake Dardanelle was divided into two areas, the upper reach and the lower reach. At normal level, the uppermost point impounded by Dardanelle Dam is located near Spadra Park. Thus, Spadra Park was used as a general reference in defining the two reaches. The upper reach, which was defined as the area from Spadra Park upstream to Ozark-Jeta-Taylor Dam, is mostly riverine with numerous navigation structures such as exposed wing dikes, submerged wing dikes, and rip rap fortified banks. Channel width is typically less than 600 m and water velocities are typically higher in the upper reach than in the lower. The lower reach, which was defined as the area from Spadra Park downstream to Dardanelle Lock and Dam 10, is characterized as mostly impounded with numerous deep holes, several large bays, and some rip-rap fortified banks. Two main tributaries, Illinois Bayou and Piney Creek flow into the lower reach. Channel width ranges from 440 to 3000 m.

Fish collection. Paddlefish were captured from April 2014 to December 2014 in 12.7 and 15.2 cm square-mesh, monofilament, tie-down gill nets that ranged in length from 50 to 100 m and ranged in depth from 3.7 m (tied down to 2.4 m) to 7.3 m (tied down to 5.5 m). Net placement was determined by searching for likely paddlefish habitat

such as deep pools, dike fields, and submerged creek channels (Crance 1987; Moen et al. 1992, Hoxmeier and Devries 1997; Wilde 2000, Zigler et al. 2003). To reduce the time that paddlefish spent in a net, nets were set during the day and checked every 4 h at minimum; more typically they were checked every hour, especially when water temperatures were higher than 16^{o}C.

The methods in which paddlefish were targeted varied between two distinct time periods. During April through July, fish were targeted throughout Lake Dardanelle. To avoid potential bias associated with capture location, collection of fish from an area ceased once six fish were tagged in that area. The Judas technique, wherein a single tagged animal is tracked to reveal the location of a congregation of animals, was minimally implemented (Cruz et al. 2009; Bajer et al. 2011). From November through December, collection techniques were altered to hasten the implantation of transmitters. Nets were deployed only in the Cabin Creek and Mill Creek areas based on telemetry readings and previous capture success. Catch per unit effort (CPUE) was standardized to average net area (203 m^2) and average soak time (3.6 h), and calculated for each set. Differences in median CPUE between the time periods were analyzed with a Wilcoxon rank-sum test.

Captured paddlefish were held in a 570 L tub filled with lake water, and fish processing began immediately after a net was checked. Each fish was laid on a flat measure and measured (±1 mm) from the anterior orbit of the eye to the fork of the caudal fin (eye-fork length, EFL). Rostrum condition was recorded. Gender was recorded if tubercles were present or if eggs were observed during surgery. Global positioning system (GPS) coordinates were recorded at each capture location with either

a Magellan Explorist 200 or a Humminbird 997c SI Combo fish finder. Water depth, surface water temperature, time, and habitat type were recorded for each set of coordinates.

Surgery. Captured paddlefish were examined to determine if they were sufficiently fit to have an ultrasonic transmitter (Sonotronics, Tuscon, Arizona) surgically implanted. Fish that exhibited lethargy, deformity, or open wounds were released without transmitters, while those that were energetic and free from sores or wounds were held for surgery. External scarring and/or lack of a complete rostrum did not disqualify a fish from implantation as long as the scars were fully healed and all other conditions were satisfied. Surgical procedures followed the methods discussed in Hart and Summerfelt (1975). Paddlefish were held slightly above the water, ventral-side up, while an incision up to 5-cm long was made along the midline, anterior to the pelvic girdle, with a sterilized scalpel, and a sterilized transmitter was inserted in to the peritoneal cavity. The incision was closed with 8-12 staples applied by a Visistat 35W surgical staple gun (Mulford 1984). Fish were injected with 20 mg/kg fish weight of oxytetracyline to reduce the chance of infection, and were released out of range of deployed gill nets once they exhibited a strong swimming response. If a fish did not exhibit a strong swimming response, or if something went wrong during surgery (eg. an internal organ was unintentionally nicked with the scalpel blade), the transmitter was removed from the fish before closing the surgical incision and releasing the fish.

Potential causes of surgery related mortality, as determined from telemetry readings, were assessed by evaluating water temperature at the time of capture, paddlefish length, surgery order (i.e., the order in which fish were implanted with a

transmitter with 1 being first, 2 being second, etc.), and transmitter size. Differences in median water temperature at the time of capture, median length, and median surgery order between paddlefish that died from surgery related causes and those that survived were each analyzed with a Wilcoxon rank-sum test. Small and medium sized transmitters were grouped together to create two classes of transmitter size, and differences in survival percentages between fish that received large transmitters and those that received small or medium transmitters were analyzed with a binomial proportions test.

Telemetry. Three sizes of transmitters were used in this study. Forty "large" model CHP-87-XL transmitters (length = 99 mm, diameter = 33.5 mm, weight = 34 g) were new and had a 3 km tracking range and a 48-month battery life; seven model CHP-87-XL transmitters were previously used and had an unknown battery life (initial battery life was 48-months); six "medium-sized" model CHP-87-L transmitters (length = 80 mm, diameter = 15.6 mm, weight = 12 g) were new and had a 1 km tracking range and an 18-month battery life; and four "small" model CHP-87-M (length = 64 mm, diameter = 15.6 mm, weight = 10 g) transmitters were new and had a 1 km tracking range and a 12 month battery life. Transmitter frequency ranged from 70 to 83 kHz. Each transmitter generated a unique aural sequence and was inscribed with a telephone number and a request to call if found.

Paddlefish were tracked within Lake Dardanelle from April 2014 through September 2015. Additional tracking forays were made into Pools 8, 9, and 12 during August, September and October of 2015 to search for fish that may have emigrated from Lake Dardanelle. Fish were located by stopping approximately every 0.5 km and scanning with a Sonotronics USR-08 ultrasonic receiver attached to a Sonotronics DH-4

directional hydrophone and/or a Sonotronics TH-2 omnidirectional hydrophone. Global positioning system (GPS) coordinates were recorded when the signal from the directional hydrophone was of equal volume in all directions at a gain setting of ≤ 5 on the receiver. Water depth, surface water temperature, water velocity (1 m below the surface), time, and macrohabitat type were recorded for each set of coordinates. When individual fish were detected in a high-use area but not pinpointed, they were assigned coordinates of the average location for that area. Average locations were determined by visually assessing the plot of all locations within a high-use area, and estimating the most representative central coordinates of each high-use area. Macrohabitat type, surface water temperature, and time were recorded for individuals assigned to average locations, but water depth and water velocity were not.

Telemetry locations were assessed to determine if implanted paddlefish were living or dead. Fish were determined to be alive if they were harvested by commercial fishermen or if they exhibited movement over time, in particular long movements (>1 km) and/or upstream movements. Fish that did not exhibit movement over time, excluding short downstream movements that may have resulted from strong current, were determined to have died from surgery-related causes. Paddlefish were censored from telemetry analyses if they were determined to have died or if their movements were inconclusive. Data from capture locations were included in appropriate analyses since the fish were alive at the time of capture.

Detection percentages were calculated by dividing the number of living paddlefish detected by the number of living paddlefish available for each month from October 2014 through September 2015. The relationship between tracking efficiency and

mean monthly flow through Lake Dardanelle was analyzed with linear regression. Mean monthly flow through Lake Dardanelle was defined as the mean of the monthly flows at Ozark Jeta-Taylor Dam and Dardanelle Dam. Mean monthly flow for each dam was calculated using daily average flows, which were obtained from the Little Rock District of the United States Army Corp of Engineers (USACE 2014).

A major high water event in the summer of 2015 created three distinct tracking periods: before, during, and after the event (Figure 1.2). Before the high water event (October 2014 – April 2015), mean monthly flow through Lake Dardanelle was 20,000 cubic feet per second (cfs) and average daily flows were typically between 10,000 and 40,000 cfs. During the high water event (May 2015 – July 2015), mean monthly flow through Lake Dardanelle was 158,000 cfs. Average daily flows were > 140,000 cfs for 76 consecutive days, peaking at 362,000 cfs in late May. After the high water event (August 2015 – September 2015), mean monthly flow through Lake Dardanelle was 22,000 cfs and average daily flows were typically between 10,000 and 40,000 cfs. Differences between mean monthly detection percentages for the periods before and after high water were analyzed with a binomial proportions test. Tracking in the riverine portion of Lake Dardanelle was not possible during high flows.

Movement. Linear range was determined for individual paddlefish by measuring the distance of the shortest path through the water between the two most distant location points over the twelve month period from October 2014 through September 2015. Seasonal linear range was determined in the same manner using locations recorded within each season plus the last location recorded in the previous season, as long as the time between the last location of the previous season and the first location of the current

season was not greater than 40 d. This approach prevented the loss of long movements that occurred inter-seasonally. Differences in median linear range among individuals, median seasonal linear range among individuals, and median seasonal linear range among seasons were each analyzed with a Kruskal-Wallis one-way analysis of variance. Pairwise comparisons between seasons were analyzed with Dunn's test.

The percent use of particular areas of Lake Dardanelle was assessed by dividing the number of detections in an area by the number of total detections in the entire lake. Areas were designated by visually assessing a density plot of all of the recorded paddlefish detections (Figure 1.3). High-use areas were defined as any area that contained ≥ 10% of the total detections, while moderate-use areas were defined as any area that contained between 4-10% of the total detections.

Reproduction. During spring 2015, paddlefish spawning migrations were investigated by increasing tracking efforts when water temperatures approached preferred spawning temperatures (12 – 16^{o}C) at three possible spawning sites: Ozark Jeta-Taylor Dam, Piney Creek, and Illinois Bayou. Water temperature at the time of spawning was determined by calculating the mean surface water temperature of all locations recorded while fish were within 12 km downstream of Ozark Jeta-Taylor Dam in February and March. Ichthyoplankton net (1 m diameter, 1 mm bar-mesh) tows were made in a downstream direction between Ozark Jeta-Taylor Dam and the mouth of O'kane Creek in April when water temperatures were between 16 and 20^{o}C in an attempt to capture larval paddlefish. Sampling effort (volume) was estimated with a mechanical flow meter (General Oceanics) attached to the mouth of the net. Egg collecting tubes

(Firehammer et al. 2006) were deployed in Piney Creek at a gravel shoal site that appeared suitable for spawning in March when water temperatures were between 11 and 13^{o}C in an attempt to capture eggs.

Habitat use. Habitat use by paddlefish in Lake Dardanelle was assessed by investigating five environmental factors: macrohabitat type, water depth, bathymetric habitat type, water velocity, and water temperature. Macrohabitat selection was analyzed with compositional analysis, which compares the proportions of available habitats to the proportions of habitats used by individuals, and produces a ranked variable sequence of habitats from most used to least used. A simplified ranking matrix, which reports the pairwise comparisons of habitats, is also produced. For this study, compositional analysis was preferable to other available methods because it uses individuals as the sample unit rather than locations, and it addresses the issue of non-independence of habitat use proportions. The analysis was conducted with Compos Analysis 6.3 Plus (Smith 2010), an Add-In for Microsoft Excel that implements the method described by Aebischer et al. (1993), and additionally weights by the square root of *n* observations for each individual. One thousand randomizations were performed, and habitat use values of zero were replaced with 0.0001.

The proportions of macrohabitat availability were calculated by delineating eight macrohabitat types (adjacent shallows, large bay, main channel impounded, main channel riverine, narrows, navigation structure, nuclear discharge bay, and tailwater; Table 1.1) onto a map of Lake Dardanelle in ArcGIS 9.0 (ESRI, Redlands, California) and dividing the area of each habitat by the total area of the lake. Individual fish were assumed to have access to all habitats each month; two individuals were observed moving nearly the

entire length of the study area in ten days or fewer, and four additional individuals were observed doing the same in 40 d or fewer. The proportions of habitats used by individual fish were determined by tracking the entirety of Lake Dardanelle once each month from October 2014 through September 2015, and overlaying the recorded paddlefish locations onto the map of macrohabitat types. In instances where fish were detected more than once per month, only the first detection was included in the analysis. No paddlefish detections were recorded in navigation structure and nuclear discharge macrohabitat types; thus, those macrohabitat types were not included in the analyses. Data collected in May and June were not included in the analysis because the upper portion of Lake Dardanelle was inaccessible due to high water. Macrohabitat selection in each season was also analyzed with compositional analysis for the same time period and in the same manner as described above. Macrohabitat types in which no paddlefish detections occurred during a given season were not included in the analysis of that season.

Water depth was measured at paddlefish locations recorded from April 2014 through September 2015. Differences in median depth among individual paddlefish were analyzed with a Kruskal-Wallis one-way analysis of variance. Differences in median depth used among seasons were analyzed with a Kruskal-Wallis one-way analysis of variance. Pairwise comparisons between seasons were analyzed with Dunn’s test. The correlation between depth and water temperature was analyzed with Spearman’s rank correlation, as was the correlation between depth and paddlefish length. To further explore water depth use, four bathymetric habitat types (pool, intermediate, shallow, and submerged creek channel; Table 1.2) were analyzed with compositional analysis for the same time period and in the same manner as the macrohabitat compositional analysis.

Bathymetric habitat types were delineated based on bathymetry maps of Lake Dardanelle as well as depth readings taken on Lake Dardanelle during this study.

Water velocity was measured at paddlefish locations recorded. Differences in median velocity among individual paddlefish were analyzed with a Kruskal-Wallis one-way analysis of variance. Differences in median velocity among seasons were analyzed with a Kruskal-Wallis one-way analysis of variance. Pairwise comparisons between seasons were analyzed with Dunn's test. The correlation between velocity and paddlefish length was analyzed with Spearman's rank correlation.

Commercial mortality. The commercial harvest rate of implanted paddlefish in Lake Dardanelle was estimated for the 2014-15 and 2015-16 commercial paddlefish seasons by dividing the number of harvested fish reported by the number of harvestable-size fish available during each season. Because fish were implanted up to 222 d prior to the start of the commercial season, length at the start of each season was estimated using an underived version of the von Bertalanffy growth equation:

$$dl / dt = K (L_\infty - l)$$

The values used for K and L_∞ were 0.191 and 1065 mm respectively, and came from the von Bertalanffy curve of combined male and female paddlefish for Lake Dardanelle (J. N. Stoeckel, Arkansas Tech University, personal communication). The commercial minimum size limit in Lake Dardanelle was 940 mm. To account for reported paddlefish that were estimated to be below the legal length limit (i.e., illegal harvest), harvest rates were estimated under two different scenarios. Under scenario one, a harvestable fish was defined as any fish $\geq$ 940 mm EFL. Paddlefish that were reported as harvested, but were estimated to be < 940 mm EFL at the start of the commercial paddlefish season were not

included in the number of reported fish. Under scenario two, a harvestable fish was defined as any fish greater than or equal to the EFL of the smallest reported paddlefish in each season. Defining a harvestable fish in this way ensured that in scenario two, all reported fish were included in the calculation of the harvest rate.

RESULTS

Fish collection. One hundred and three paddlefish were captured in 173 gill net sets from seven different sites in Lake Dardanelle from April 12, 2014 to December 7, 2014. Average gill net area was 35,170 m^2, while average soak time was 3.6 h. Total CPUE, standardized to average net area (203 m^2) and average soak time (3.6 h), was 0.76 (SD=2.10). The 156 sets that were made before monthly tracking began caught 65 paddlefish and had a CPUE of 0.50 (SD=1.71). The remaining 17 sets that were made after monthly tracking began caught 38 paddlefish and had a CPUE of 3.13 (SD=3.49). Catch per unit effort for sets before tracking began was significantly different than CPUE for sets after (W = 411, P < 0.001). Paddlefish ranged in length from 665 to 1181 mm EFL (n = 103, median = 887). Fifty percent of the fish were between 825 and 948 mm in length.

Surgery. Fifty-seven paddlefish were implanted with ultrasonic transmitters. Two fish were gravid females, while the gender of the remaining 55 fish was unknown. Forty-seven of the fish received large transmitters; six received medium-sized transmitters; and four received small transmitters. Implanted paddlefish ranged in length from 750 to 1100 mm EFL (median = 880 mm). Fifty percent of the fish were between 825 and 947 mm in length. Water temperature at the time of capture for implanted fish

ranged from 8.3 to 28.9 °C (median = 16.7 °C). Fifty percent of the water temperatures at capture were between 15.0 and 25.6 °C.

Twelve (21.1%) paddlefish died from surgery-related causes as determined from telemetry readings. Fish that lived were not captured at significantly different water temperatures than fish that died (W = 228, P = 0.902). Eye to fork length was not significantly different between fish that lived and those that died (W = 222, P = 0.790). Capture order was not related to whether fish lived or died (W = 253, P = 0.685). Transmitter size, when small and medium-sized transmitters were combined, was not significantly different between fish that lived and fish that died (X^2 = 253, P = 0.123).

Telemetry. Implanted paddlefish were captured from five different sites in Lake Dardanelle. Of the 57 paddlefish that received transmitters, 18 (32%) were censored from telemetry analyses due to surgery related mortality (n = 12, 21%) or inability to determine if fish were alive (n = 6, 10%). Four hundred locations were recorded from April 2014 to September 2015 for the remaining 39 (68%) fish (Figure 1.4). The number of locations per individual fish ranged from 0-14. Mean monthly detection percentage for October 2014 through September 2015 was 67% and ranged from 25% to 95%. Monthly detection percentage was negatively correlated with mean monthly flow from Ozark Jeta-Taylor Dam (slope = 0.826, df = 11 P = 0.004, adjusted r^2 = 0.575; Figure 1.5).

Monthly detection percentage was 85% before the high water event, and dropped to 35% during high water. After the high water event, flows returned to normal levels, but monthly detection percentage remained low at 50%. Detection percentages before and after high water were statistically different (X^2 = 33, P < 0.001). Fourteen fish were

never tracked within Lake Dardanelle after June 2015, indicating that some fish may have emigrated during the high water period.

Movement. Emigration from Lake Dardanelle was confirmed when two implanted paddlefish were detected immediately below Dardanelle Dam in October 2015. The fish were last tracked within Lake Dardanelle in May 2015 and June 2015 respectively, indicating that emigration took place during the high water event of summer 2015. Tracking forays into Pools 8 and 12 did not result in any paddlefish detections.

Linear range did not differ among individuals during the twelve month period from October 2014 through September 2015 ($X^2 = 34$, $P = 0.468$; Table 1.3), or during fall, winter, spring, or summer of the same time period (all $P > 0.0455$; Table 1.3). Spring linear range was significantly higher than fall ($P = 0.014$), summer ($P < 0.000$), and winter ($P < 0.000$) linear ranges (Figure 1.6). Fall linear range was significantly higher than winter ($P = 0.011$) and summer ($P = 0.020$) linear ranges (Figure 1.6). Winter and spring linear ranges were not significantly different ($P = 0.486$; Figure 1.6).

Paddlefish were detected in some areas much more frequently than others. Four high-use areas (Cabin Creek, Lake Dardanelle State Park, Cane Creek, and Piney Bay; Figure 1.4) were identified and accounted for 68% of all detections. Four moderate-use areas (Ozark Dam Tailwater, Piney Narrow, Piney Mouth, and Dardanelle Dam; Figure 1.4) were identified and accounted for 20% of all detections. The number of different areas that an individual was detected in ranged from two to seven ($n = 35$, median = 4); 75% of all paddlefish used three or more areas. Eleven (31.4%) paddlefish showed fidelity (> 50% of an individual’s detections occurred in one area) to an area; nine of those individuals showed fidelity to the Cabin Creek area, while the remaining two

showed fidelity to either the Cane Creek or Piney Bay areas. Use varied among areas; some paddlefish frequently moved between multiple high-and moderate use areas, while others rarely strayed from a single high-use area. A typical individual used between one and three adjacent high- or moderate-use areas.

Reproduction. Distinct upstream movements, presumably spawning migrations, were observed for nine out of 36 (25%) individuals. Paddlefish were detected in the section of Lake Dardanelle that is upstream of the mouth of Six Mile Creek in February, March, and April 2015. Notably, with the exception of the tailwater pool directly below Ozark Jeta-Taylor Dam, no paddlefish were detected in this section outside of spawning season. Three additional fish may have made spawning migrations, as they were not detected during monthly tracking in March, April, and May, possibly due to inefficiency of ultrasonic tracking in turbulent water (as found below Ozark Jeta-Taylor Dam in spring) and/or emigration to pools above Lake Dardanelle. Mean water temperature was 6.5^{o}C (n = 9) at the locations recorded immediately prior to spawning runs in February and early March. Mean water temperature was 13.0^{o}C (n = 27) at the locations recorded during spawning runs (i.e., within 12 km below Ozark Jeta-Taylor Dam) in February through early April. Mean water temperature was 18.0^{o}C (n = 5) at the locations recorded immediately after spawning runs in late March and April. Distinct spawning runs were not detected in Piney Creek or Illinois Bayou, although paddlefish were detected farther upstream each tributary arm during the spring than during any other season.

The fish that made spawning runs were dispersed throughout a 12.0 km stretch below Ozark Jeta-Taylor Dam while water temperatures were within spawning range, but

moved within 4.0 km of the dam during a pulse of higher flow (~1.0 m/s) in late March. During this pulse, a possible spawning site was identified 3.9 km below Ozark Jeta-Taylor Dam when four fish were detected in close proximity (within 100 m) of each other. The site had bedrock substrate and water temperature was 13.1^{o}C at the time of detection. Six of the nine fish that made spawning migrations moved back downstream after spawning, while the three remaining fish were never detected again after mid-April.

Horizontal ichthyoplankton net tows were conducted 1 m below the surface between Ozark Jeta-Taylor Dam and the mouth of Okane Creek in April 2015 when water temperatures were between 16.7 and 19.4^{o}C. A total of 127,900 m^3 of water were sampled, but no paddlefish larvae or eggs were collected. Eggs were also not collected when 16 egg collecting tubes (Firehammer et al. 2006) were deployed in Piney Creek for 48 h in late March 2015 when water temperatures were between 11.1 and 12.7^{o}C.

Habitat use. Macrohabitat selection was analyzed with compositional analysis for the 12-month period from October 2014 through September 2015 (Table 1.4). Paddlefish were never detected in the nuclear discharge bay or near navigation structure habitats; thus, those macrohabitats were not included in the analysis. Paddlefish did not select macrohabitats at random during the year ($\Lambda = 0.149$, $X^2 = 72.48$, $P < 0.001$). The macrohabitat ranked variable sequence for the year, from most used to least used, was: main channel impounded > tailwater > narrows > large bay > main channel riverine >>> adjacent shallows (“>>>” denotes statistical difference). The ranking matrix for the year was used to determine the following differences between macrohabitat types that were not indicated by the ranked variable sequence: paddlefish significantly selected for main channel impounded macrohabitat more than all other macrohabitat types except for

tailwater; tailwater, narrows, large bay, and main channel riverine habitats were not significantly different from each other (Figure 1.7).

Macrohabitat selection was also analyzed with compositional analysis for winter, spring, summer, and fall of the same 12-month period (Table 1.4). Nuclear discharge and navigation structure macrohabitats were omitted from the analysis due to a lack of detections in those macrohabitats. Additional macrohabitats were also omitted from seasonal compositional analyses if no detections occurred within a macrohabitat during the season being assessed. Paddlefish did not select macrohabitats at random during winter ($\Lambda = 0.632$, $X^2 = 16.08$, $P = 0.001$), spring ($\Lambda = 0.137$, $X^2 = 63.63$, $P < 0.001$), summer ($\Lambda = 0.290$, $X^2 = 26.00$, $P < 0.001$), or fall ($\Lambda = 0.530$, $X^2 = 24.13$, $P < 0.001$). Main channel impounded and tailwater macrohabitats were the most selected macrohabitats in all seasons except for summer when main channel impounded and large bay habitats were the most selected. Adjacent shallows macrohabitat was the least selected macrohabitat in spring and summer (no detections occurred in adjacent shallows macrohabitat in winter or fall). Large bay macrohabitat showed the most seasonal variability in rank; it ranked third in winter, fourth in spring, second in summer, and fifth in winter. Narrows macrohabitat also varied seasonally; detections in narrows macrohabitat only occurred in fall, when it ranked third. Main channel riverine was ranked as one of the three least selected macrohabitats in all seasons. The ranked variable sequences for each season were never the same, indicating that paddlefish selected different macrohabitats at different times of the year (Figure 1.7).

Paddlefish generally preferred deep (>9) or intermediate-depth (6-9 m) water. Water depth at paddlefish locations ranged from 1.7 to 18.4 m ($n = 292$, median = 8.0 m).

Fifty percent of water depth measurements were between 5.4 and 11.5 m. Median water depth for individual paddlefish ranged from 3.5 to 13.7 m, but did not differ among individual paddlefish ($X^2 = 48$, $P = 0.055$). Median water depth was 10.2, 6.8, 7.3, and 8.8 m in winter, spring, summer, and fall respectively, and differed among seasons ($X^2 = 11.7$, $P = 0.008$). Water depth was significantly greater in winter than in spring ($P = 0.004$) and summer ($P = 0.036$), and significantly greater in fall than in spring ($P = 0.048$). All other season comparisons were not statistically different (all $P > 0.121$). Paddlefish occupied deeper water when water temperatures were lower; water depth had a weak negative correlation with water temperature at paddlefish locations ($r_s = -0.282$, $n = 285$, $P < 0.001$). Length was not correlated with water depth occupied ($r_s = 0.016$, $n = 292$, $P = 0.791$).

To further explore water depth use, four bathymetric habitat types were analyzed with compositional analysis for the same time periods as macrohabitat types (Table 1.5). Paddlefish did not select bathymetric habitats at random during the year ($\Lambda = 0.473$, $X^2 = 28.49$, $P < 0.001$). The bathymetric ranked variable sequence for the year, from most used to least used, was: pool >>> intermediate > submerged creek channel > shallow (“>>>” denotes statistical difference). Based on the ranking matrix for the year, intermediate habitat was selected significantly more than shallow habitat. Paddlefish did not select bathymetric habitats at random during winter ($\Lambda = 0.381$, $X^2 = 33.75$, $P = 0.001$), spring ($\Lambda = 0.691$, $X^2 = 11.83$, $P = 0.008$), or fall ($\Lambda = 0.445$, $X^2 = 30.75$, $P < 0.001$). Use was random during summer ($\Lambda = 0.731$, $X^2 = 6.59$, $P = 0.086$). The seasonal ranking matrices showed that pool habitat was selected significantly more than

all other bathymetric habitat types in winter and fall, and shallow habitat was selected significantly less than all other habitat types in winter and spring (Figure 1.8).

Paddlefish generally preferred slow (0.10 m/s) water velocities. Surface water velocity at paddlefish locations ranged from 0.00 to 1.08 m/s (n = 270, median = 0.06 m/s). Seventy-five percent of all measured water velocities were ≤0.19 m/s. Water velocity did not differ among individual paddlefish (X^2 = 43.79, df = 34, P = 0.121). Median water velocity was 0.04, 0.19, 0.06, and 0.04 m/s for winter, spring, summer, and fall respectively, and differed among seasons (X^2 = 85.13, df = 3, P < 0.001). Median water velocity was different for all pairwise comparisons (all $P \leq 0.001$) except fall versus winter (P = 0.481). Paddlefish lengths and the water velocities at fish locations were not correlated (r_s = -0.005, n = 270, P < 0.936). The amount of flow through Lake Dardanelle and the water velocity at fish locations had a strong positive correlation (r_s = 0.724, n = 182, P < 0.001).

Commercial mortality. Three implanted paddlefish were reported as harvested by commercial fishermen in Lake Dardanelle during the 2014-15, while one was reported during the 2015-16 season. Two of the three fish reported during the 2014-15 season were calculated to be of legal harvestable size (estimated EFL = 945 and 1004 mm), while one of the fish was not (estimated EFL = 888). The single fish reported during the 2015-16 season was not calculated to be of legal harvestable size (estimated EFL = 912). Thus, two scenarios were used to estimate the commercial fishing mortality rate in Lake Dardanelle for each commercial fishing season. Under scenario one, in which the number of harvestable fish included only fish ≥940 mm EFL, the harvest rate was 17% (2/12) and 0% (0/6) in the 2014-15 and 2015-16 seasons respectively. Under scenario

two, in which the number of harvestable fish included all fish with an EFL greater than or equal to the smallest harvested paddlefish, the harvest rate was 15% (3/20) and 9% (1/11) in the 2014-15 and 2015-16 seasons respectively. The smallest harvested paddlefish during the 2014-15 and 2015-16 seasons were estimated to be 888 and 912 mm respectively. No paddlefish were reported as harvested by recreational fishermen.

DISCUSSION

Fish collection—Targeting paddlefish for capture was six times more effective after tracking began than before. The simple explanation for this discrepancy is that during the period before tracking began, a high amount of effort was expended in areas where paddlefish were infrequent, and during the period after tracking began, only the two most frequently used areas were targeted. While this explanation is straightforward, the dramatic increase in CPUE is ascribable to knowledge gained from telemetry activities, and demonstrates the applicability of such information. Comparisons of CPUE with other studies such as Paukert and Fisher (1999, 2000) are not appropriate because sampling was not random in my study.

Given that approximately half of the telemetered paddlefish were captured from the Cabin Creek area, bias associated with capture location was initially a concern. However, for 60% of individuals, the most frequently used area was not the same as the area it was tagged in, indicating that capture location bias was probably not an issue. Furthermore, Cabin Creek was an important area for all fish regardless of where they were caught, and fish captured in the Cabin Creek area distributed throughout Lake Dardanelle similarly to those captured elsewhere.

Surgery mortality. Twelve (21%) implanted paddlefish died from surgery related causes. This number may be an overestimate because at least three months elapsed between surgery and the start of tracking for seven of the fish. During this time, some of the fish may have expelled transmitters or died from anthropogenic activities such as boating or commercial nets, as noted in other studies (Wilde 2000; Zigler 2003; Firehammer and Scarnechia 2006a). Natural mortality is low for adult paddlefish in the central part of their range (Boone and Timmons 1995; Timmons and Hughbanks 2000; Donabauer 2007) and likely did not account for any of the mortalities in this case. Recreational fishing mortality was also unlikely to contribute, as it probably occurs only in Lake Dardanelle during spring spawning migrations. Surgical mortality of paddlefish varies in the literature, but is generally lower than what I reported. Donabauer (2007) and Southall (1982) reported 3% and 18% surgical mortality respectively. Zigler et al. (2003) reported 0% surgical mortality, but noted that 27% of transmitters became stationary between two and twenty-one months post-surgery. Neither Stancill et al. (2002) nor Firehammer and Scarnecchia (2006a) reported any surgical mortality in their respective telemetry studies.

No specific causes of surgical mortality were determined. I expected higher water temperatures at time of capture to result in higher rates of surgical mortality because other studies have reported increased gillnet mortality in paddlefish at water temperatures >10°C (Paukert and Fisher 2001; Bettoli and Scholten 2006). However, there was no relationship between water temperature at the time of capture and surgical mortality (P = 0.902). It is noteworthy to point out that nearly all surgeries occurred at water temperatures >10°C. Perhaps 10°C is a threshold above which paddlefish are uniformly

susceptible to handling. Paddlefish size and capture order (i.e., surgeon experience) were also unrelated to surgical mortality ($P = 0.790$ and $P = 0.685$ respectively). Although transmitter size was not significantly related to surgical mortality ($P = 0.123$), all of the paddlefish that died from surgery were implanted with large transmitters. The sample size of combined small and medium transmitters ($n = 9$) was apparently too small to show significance. I suspect that transmitter size influenced surgery mortality via incision size and surgery duration, both of which increase as transmitter size increases. Incision size for small and medium-sized transmitters was approximately 2 cm, compared to approximately 5 cm for large transmitters. Factors that could not be measured, such as the length of time a fish was entangled in the gill net, may have also played a role in surgery mortality. I am unaware of any studies that analyzed specific causes of post-surgery mortality.

Movement. Emigration from Lake Dardanelle was confirmed for two telemetered paddlefish, both of which were detected below Dardanelle Dam in October 2015. Twelve other paddlefish likely emigrated as well, as they were never detected in Lake Dardanelle after June 2015. Assuming a monthly detection percentage of 80%, the probability that a fish would go undetected for three consecutive months is <1%. Numerous studies have shown that paddlefish are capable of moving long distances, both upstream and downstream, even when dams are present (Rosen et al. 1982; Southall and Hubert 1984; Moen et al. 1992; Stancill et al. 2002; Zigler et al. 2004; Donabauer 2007; Mettee et al. 2009; Pracheil et al. 2012). The movement of fish between adjacent pools of the Arkansas River in this study shows that populations are not completely separate.

However, Leone et al. (2012) found that population characteristics varied among adjacent pools, so movement is probably limited.

Paddlefish emigration from Lake Dardanelle was apparently facilitated by the major high water event that occurred from May through July 2015. Zigler et al. (2004) reported that more paddlefish passed through dams on the upper Mississippi River during strong flood pulses than during weak flood pulses. During a study in which no major floods occurred, Donabauer et al. (2009) reported emigration rates (5 – 13%) much lower than those found in this study. I suspect that the missing paddlefish moved a considerable distance downstream, because the high water event took place well after spawning, and both confirmed emigration events occurred in the pool below Lake Dardanelle. Furthermore, passage through a dam is probably easier in a downstream direction. Stancill et al. (2002) hypothesized that paddlefish may have historically made extensive downstream movements prior to the presence of dams. Rosen et al. (1982) and Stancill et al. (2002) both reported downstream paddlefish movements >1,900 river km.

Habitat selection. Main channel impounded habitat was ranked by compositional analysis as the most used macrohabitat type, and while it comprised 32% of the total lake area, it accounted for nearly half (47%) of all paddlefish detections. Within main channel impounded habitat, paddlefish concentrated in the deeper pools and seldom used shallower areas. The most frequently used area in Lake Dardanelle, as well as two moderate use areas, occurred within main channel impounded habitat. Use of main channel impounded habitat was similar in all seasons, as was paddlefish distribution within the habitat. Paddlefish use of impounded portions of reservoirs varies. Zigler et al. (2003) found that paddlefish selected impounded areas in Pool 8 of the Mississippi

River but avoided them in Pool 5. Paukert and Fisher (2001) reported substantial use of the main pool of Keystone Reservoir on the Arkansas River, while Donabauer (2007) observed that impounded portions of Ozark Lake and Pool 13 on the Arkansas River were not used extensively.

Tailwater habitat was ranked by compositional analysis as the second most used macrohabitat type. This ranking was clearly influenced by the limited availability of tailwater habitat (<1% of the total lake area), and may be artificially high in regard to importance, especially when one considers that tailwater habitat only accounted for 4% of paddlefish detections, the majority of which occurred during spring spawning migrations. Moreover, Ozark Dam served as a substantial barrier that may have concentrated fish attempting to move upstream. While some studies have reported that paddlefish prefer tailwater habitat (Southall and Hubert 1984; Moen et al. 1992; Zigler et al. 2003), other studies have reported little to moderate use outside of the spawning season (Zigler et al. 1999; Donabauer 2007). I suspect that tailwater habitat in Lake Dardanelle is not important for paddlefish outside of the spawning season because it is lower in quality (i.e., more shallow) than other habitat types.

Large bay habitat was ranked by compositional analysis as the fourth most used macrohabitat type. Percent usage (24%) was similar to percent availability (24%), indicating that use of large bay habitat was random. However, 87% of paddlefish detections in large bay habitat occurred in only two bays, Piney Bay and the Illinois Bayou arm, while the three remaining bays were rarely used. Additionally, Piney Bay and the Illinois Bayou arm contained the second and fourth most frequently used areas in Lake Dardanelle respectively. Consequently, large bay habitat is probably more

important than the analysis suggested. I suspect that paddlefish used Piney Bay and the Illinois Bayou arm because those bays are where the two largest tributaries to Lake Dardanelle enter the reservoir. Donabauer (2007) reported frequent use of a major tributary mouth in Ozark Lake on the Arkansas River. Piney Creek and Illinois Bayou probably affect zooplankton production within their respective bays via nutrient input and water clarity. Paddlefish selection of large bay habitat varied seasonally. Selection for large bays was lowest in the winter, perhaps due to the lack of deep pools in which paddlefish concentrated during winter. Selection was highest in the summer; paddlefish may have been using large bays as a refuge from the high water velocities of the main channel during the summer flood event. Alternatively, there may have been some sampling bias that favored off channel habitats during flooding because tracking conditions were better there (i.e., the water was less turbulent). Other studies that investigated paddlefish habitat use did not analyze habitat types similar to the large bay habitat type in my study.

Compositional analysis ranked bathymetric habitat types, from most used to least used, as follows: pool >>> intermediate > submerged creek channel >>> shallow (where “>>>” denotes a significant difference). Combined pool and intermediate habitats comprised only 18% of the total lake area, but accounted for 69% of paddlefish detections. Conversely, shallow habitat comprised 82% of the total lake area, but only accounted for 23% of paddlefish detections. Of the eight high or moderate-use areas, four were deep pools and two were pools of intermediate depth. Paddlefish clearly selected deeper pools and avoided shallow areas in Lake Dardanelle. These findings concur with numerous other studies that have reported the use of deep water by

paddlefish (Moen et al. 1992; Zigler et al. 1999, 2003; Paukert and Fisher 2001; Stancill et al. 2002). Submerged creek channel habitat comprised 1% of the total lake area, and accounted for 9% of paddlefish detections. Use of submerged creek channel habitat may have been underestimated because the habitat was narrowly defined, meaning that small errors in detection accuracy could have resulted in lower counts. Yet, it is unclear whether paddlefish were detected at submerged creek channels because they preferred them or because they were drawn to the large tributary bays in which submerged creek channels occurred. While other paddlefish habitat studies do not mention submerged creek channels, Donabauer et al. (2009) reported that impounded creek channel habitat was used during the summer, but avoided during other seasons. Use of bathymetric habitat types by season varied only slightly; paddlefish used pool habitat more in the winter, while intermediate depth use increased in the spring as fish moved to shallower upstream areas during spawning.

Reproduction. Nine (25%) paddlefish were observed migrating upstream to spawn below Ozark Jeta-Taylor Dam in March and April 2015. I expected 50-75% of implanted paddlefish to make spawning migrations because female paddlefish in the lower Arkansas River do not spawn every year (Donabauer 2007), but most males probably do (Paukert and Fisher 2001b; Firehammer and Scarnecchia 2006b). The low percentage of spawning fish that I observed may be due to unfavorable spawning conditions (eg. low flows) during spring 2015, but may also indicate that paddlefish were spawning elsewhere. Piney Bay had the highest concentration of paddlefish detections in Lake Dardanelle during March and April, making it the most likely alternate spawning

location. Gravel beds suitable to paddlefish spawning (Purkett 1961, Paukert and Fisher 2001b) were detected in Piney Creek just upstream from the bay.

Initial paddlefish spawning migrations were apparently triggered by a flood pulse (~100,000 cfs) that began on March 14. Water temperatures during the pulse were approximately 9 to 10^{o}C. The pulse was short-lived (four days), and paddlefish retreated to downstream staging areas within 12 km of the dam. Other studies have reported that paddlefish spawning movements are initiated by increased flows (Wallus 1986; Lein and Devries 1998; Firehammer and Scarnecchia 2006a) and that paddlefish retreat back downstream when flows decrease substantially (Firehammer and Scarnecchia 2006b). A possible spawning site was identified 3.9 km below the dam when four fish were observed within close proximity of one another during a small flood pulse (~40,000 cfs). The site was approximately 3 m deep and had bedrock substrate; water temperature was 13.1^{o}C at the time of detection. O'Keefe (2007) collected paddlefish eggs at a similar location in the Tennessee-Tombigee Waterway that was >3 m deep and had bedrock substrate. Paddlefish moved back to the lower portions of Lake Dardanelle in April and May when water temperatures were above 18^{o}C. This finding concurs with Donabauer (2007), who reported that gravid females in Ozark Lake retreated from spawning areas at water temperatures above 19^{o}C.

I suspect that paddlefish regularly spawn at or below Ozark Jeta-Taylor Dam, even though it could not be confirmed by collecting larvae or eggs. Homing and spawning site fidelity in paddlefish have been suggested (Lein and DeVries 1998; Stancill et al. 2002); therefore, the observed spawning runs, in and of themselves, may be evidence of previous spawning success. Moreover, Donabauer (2007) confirmed

successful spawning in Ozark Lake below James W. Trimble Dam, which is very similar to Ozark Jeta-Taylor Dam.

Commercial harvest.—Four paddlefish were reported as harvested by commercial fishermen on Lake Dardanelle, three during the 2014-15 season and one during the 2015-16 season. Because two of the fish were estimated to be below the legal length limit, commercial mortality was estimated under two scenarios. Mean weighted commercial mortality across both seasons was 11% (2/18) under scenario one, which only included fish estimated to be of legal harvestable size. Mean weighted commercial mortality across both seasons was 13% (4/31) under scenario two, which expanded to include all fish with an EFL greater than or equal to the smallest harvested fish. Scenario one clearly underestimates commercial mortality because it does not include all of the fish that were harvested. Scenario two provides a more realistic estimate, but assumes that commercial fishermen were not always following legal length limits. Quinn et al. (2009) reported multiple length violations during four special commercial seasons on Ozark Lake and Pool 13 in the Arkansas River, even though fishermen were required to undergo daily checks by the AGFC. Commercial mortality under scenario two may still be underestimated, as voluntary tag return rates are notoriously low (Matlock 1981; Green et al. 1983). However, the estimates of commercial mortality that I determined were well within the range of other studies. Donabauer (2007) reported a commercial harvest of 23% in Ozark Lake and Pool 13 on the Arkansas River during a 10 day commercial season; Timmons and Hugh banks (2000) reported a commercial harvest rate of 13% and 7% in Kentucky Lake and Berkley Lake respectively; and Hageman (1986) reported a commercial harvest rate of 27% in Lake Cumberland. Based on my findings,

paddlefish may be overfished in Lake Dardanelle. While exploitation rates ≤15% have generally been considered acceptable in the past (Jennnings and Zigler 2000), more recent studies have suggested that exploitation rates less than 15% can result in a reduction in spawning potential (Scholten and Bettoli 2005; Pierce et al. 2015).

CONCLUSIONS

Paddlefish in Lake Dardanelle preferred deep pools and large tributary bays. Paddlefish movement and habitat use in Lake Dardanelle were explained by a density plot of paddlefish locations (Figure 1.3), which clearly revealed high and moderate-use areas. Compositional analysis of macrohabitat type selection did not explain why paddlefish preferred particular areas, because paddlefish apparently did not select locations based on macrohabitat type. Conversely, analysis of bathymetric habitat type thoroughly explained paddlefish locations. Depth appears to be a much more important factor than macrohabitat type when predicting paddlefish location. I agree with Zigler et al. (2003), who stated that relying on "aquatic area types to describe paddlefish habitat… may be inadequate for making management decisions regarding critical habitats for paddlefish in complex systems" (p. 203). Future studies of paddlefish habitat selection should focus on refining habitat definitions, with special emphasis on depth and current velocity as well as habitat type. Additionally, standardized paddlefish habitat definitions for river and reservoir systems would improve inter-study comparisons.

Paddlefish in Lake Dardanelle almost certainly spawn in the Ozark Jeta-Taylor Dam tailwater, but may also spawn in other areas, primarily Piney Creek. Confirming reproduction in the tailwater, and investigating other potential spawning cites would

enable fisheries managers to protect critical spawning habitat and ensure viable paddlefish populations.

Paddlefish may be overfished in Lake Dardanelle. My estimate of commercial mortality (13%) is probably conservative, because it does not account for non-reporting of transmitters. The additive effect of recreational fishing mortality alone almost surely pushes paddlefish harvest above the commonly accepted limit of 15%. Furthermore, I saw evidence that legal length limits were not being adhered to, which may decrease the probability of paddlefish reaching maturity and spawning.

The creation of a refuge area within Lake Dardanelle could potentially reduce harvest levels, increase spawning success, and convey the importance of conservation to resource users. Piney Bay is an ideal candidate for such a refuge because it is used by paddlefish year-round, it contains potential spawning sites, and its boundaries are clearly defined making regulations easy to implement.

I recommend that fisheries managers consider the following actions: (1) assess recreational mortality, (2) increase enforcement of commercial length limits to ensure that paddlefish have the opportunity to spawn, and (3) consider designating Piney Bay as a refuge where commercial fishing is prohibited year-round.

TABLES

Table 1.1: Descriptions of eight macrohabitat types available in Lake Dardanelle, Arkansas River, Arkansas.

Habitat Type	Code	Description
Adjacent Shallows	AS	Waters adjacent to the main channel that are typically less than 3 m deep. Includes small bays, flats, and backwaters.
Large bays	LB	A bay that is greater than 1 square kilometer. (Shoal Bay, Piney Bay, Goose Island Bay, Delaware Bay, Dardanelle Bay, and Illinois Bayou Bay)
Main channel impounded	MI	The area impounded by Dardanelle Dam that typically has current at normal river levels (20,000 - 50,000 cfs) and is generally deeper than 3 m. Includes navigation channels.
Main channel riverine	MR	The area that is not impounded by Dardanelle Dam, typically has current at normal river levels (20,000 - 50,000 cfs), and is generally deeper than 3 m. Includes navigation channels.
Narrows	NR	An impounded creek channel that is constrained in width by a steep canyon. Typically less than 200 m wide and greater than 5 m deep.
Navigation structures	NS	The areas within 20 m of a wing dike and downstream dike fields.
Nuclear discharge bay	ND	The bay that receives discharge from Nuclear Power One. Water temperatures are regularly higher than average water temperatures in the rest of Lake Dardanelle.
Tailwaters	TW	The area from Ozark Jetta-Taylor Dam downstream 715 m and the area from the waterworks dam on Illinois Bayou downstream 130 m.

Table 1.2: Descriptions of eight bathymetric habitat types available in Lake Dardanelle, Arkansas River, Arkansas.

Habitat Type	Code	Description
Pool	PL	A contiguous area that is ≥9 m deep and larger than 300,000 m^2.
Intermediate	INT	A contiguous area that is between 6 and 9 m deep, and larger than 300,000 m^2.
Shallow	SH	Waters that are ≤6 m deep.
Submerged creek channel	SCC	The historic channels of Piney Creek and Illinois Bayou that are submerged within their respective bays. Typically between 6 and 11 m deep, 60 m wide, and surrounded by shallow (<6 m) flats.

TABLE 1.3—Linear ranges for telemetered paddlefish in Lake Dardanelle, Arkansas for five different time periods, October 2014 through September 2015.

	Linear Range (km)		
Period	Minimum	Median	Maximum
Year	5.4	25.7	77.3
Winter	0.1	1.9	38.3
Spring	0.2	20.9	81.1
Summer	0.2	1.3	21.9
Fall	0.1	9.7	76.4

Table 1.4: Macrohabitat selection of paddlefish in Lake Dardanelle, Arkansas from October 2014 through September 2015, as determined by compositional analysis. Ranked variable sequences, from most used (1) to least used (6), are shown in bold. Shaded blocks denote macrohabitat types that were not significantly different from each other. Macrohabitat types in which paddlefish were not detected were omitted from the analysis.

	Macrohabitat rank					
Period	1	2	3	4	5	6
Year	**MI**	**TW**	**NR**	**LB**	**MR**	**AS**
n=38	MI	TW				
		TW	NR	LB	MR	
						AS
Winter	**TW**	**MI**	**LB**	**MR**		
n=35	TW	MI				
		MI	LB	MR		
Spring	**TW**	**MI**	**MR**	**LB**	**AS**	
n=32	TW	MI				
		MI	MR	LB		
					AS	
Summer	**MI**	**LB**	**MR**	**AS**		
n=21	MI	LB				
		LB	MR			
			MR	AS		
Fall	**MI**	**TW**	**NR**	**MR**	**LB**	
n=38	MI	TW	NR			
			NR	MR		
				MR	LB	

[a]Refer to Table 1.1 for habitat abbreviations.

Table 1.5: Bathymetric habitat selection of paddlefish in Lake Dardanelle, Arkansas from October 2014 through September 2015, as determined by compositional analysis. Ranked variable sequences, from most used (1) to least used (4), are shown in bold. Shaded blocks denote macrohabitat types that were not significantly different from each other. Bathymetric habitat selection was random during summer ($\Lambda = 0.731$, $X^2 = 6.59$, $P = 0.086$); thus, it was not included.

	Macrohabitat rank			
Period	1	2	3	4
Year	**PL**[a]	**INT**	**SCC**	**SH**
n=38	PL			
		INT	SCC	
			SCC	SH
Winter	**PL**	**SCC**	**INT**	**SH**
n=35	PL			
		SCC	INT	
				SH
Spring	**INT**	**PL**	**SCC**	**SH**
n=32	INT	PL	SCC	
				SH
Fall	**PL**	**INT**	**SCC**	**SH**
n=38	PL			
		INT	SCC	SH

[a]Refer to Table 1.2 for habitat abbreviations.

FIGURES

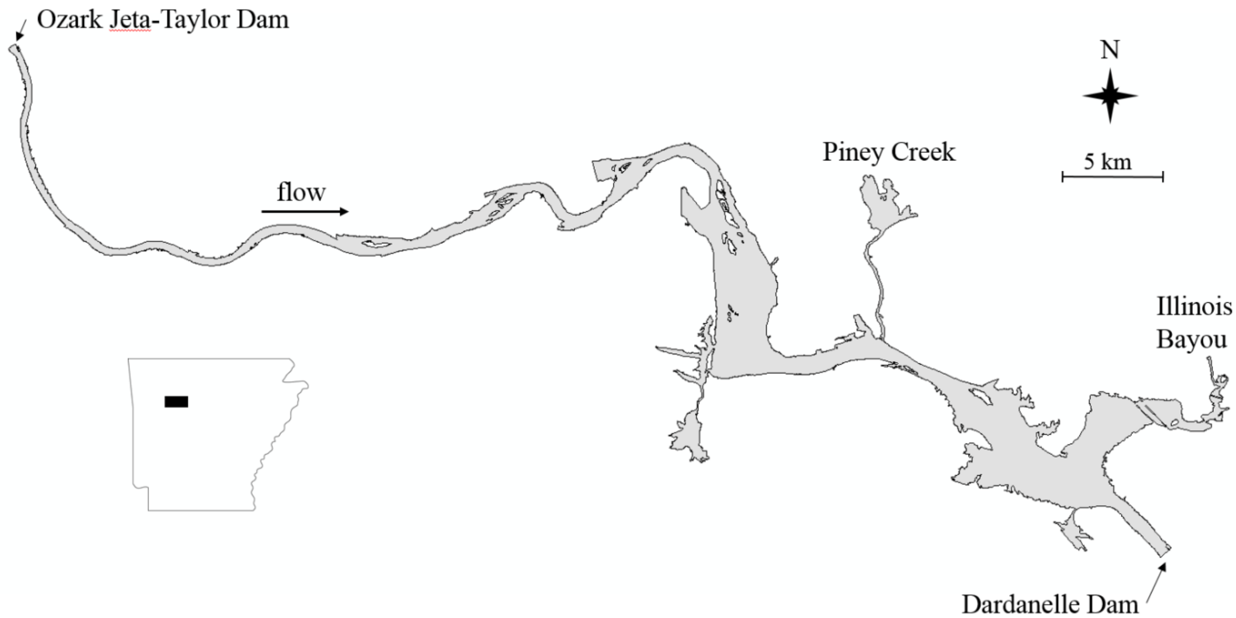

Figure 1.1: The study area, Lake Dardanelle, Arkansas.

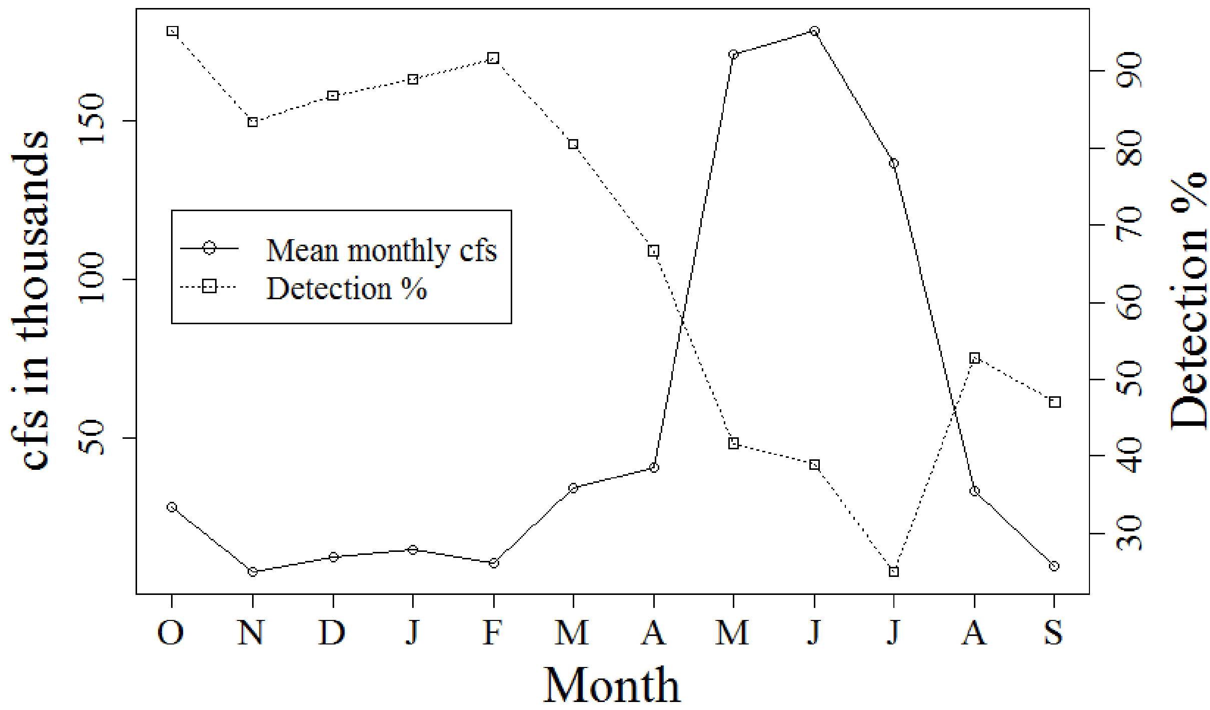

Figure 1.2: Percentage of paddlefish detected each month and mean month flow, October 2014 through September 2015, in Lake Dardanelle Arkansas.

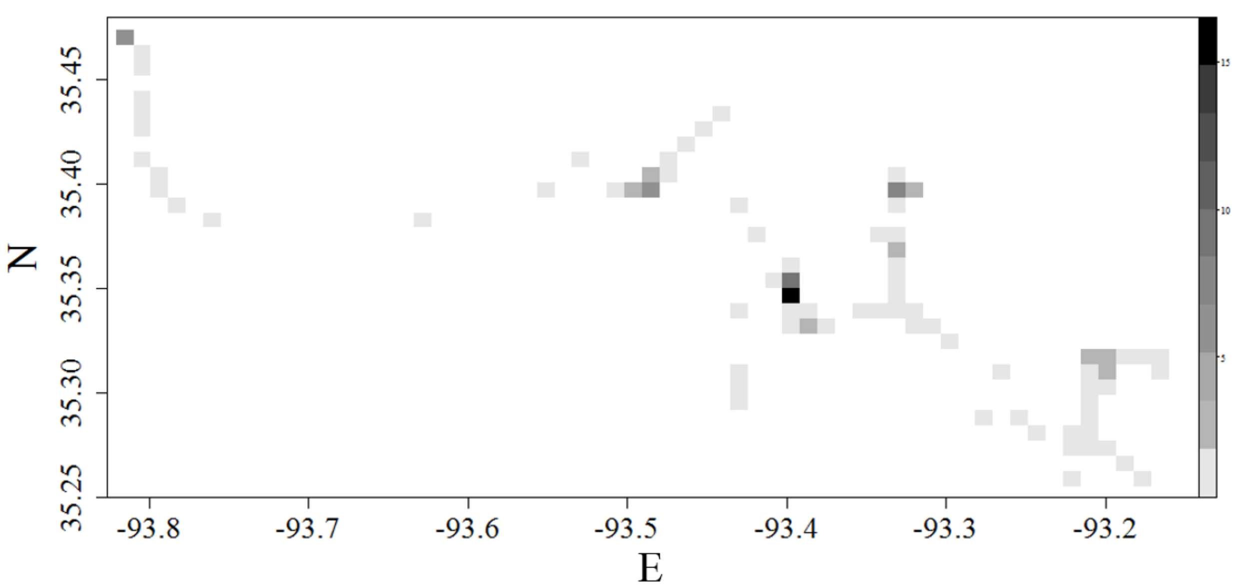

Figure 1.3: Density plot of paddlefish locations recorded from April 2014 through October 2015 in Lake Dardanelle, Arkansas.

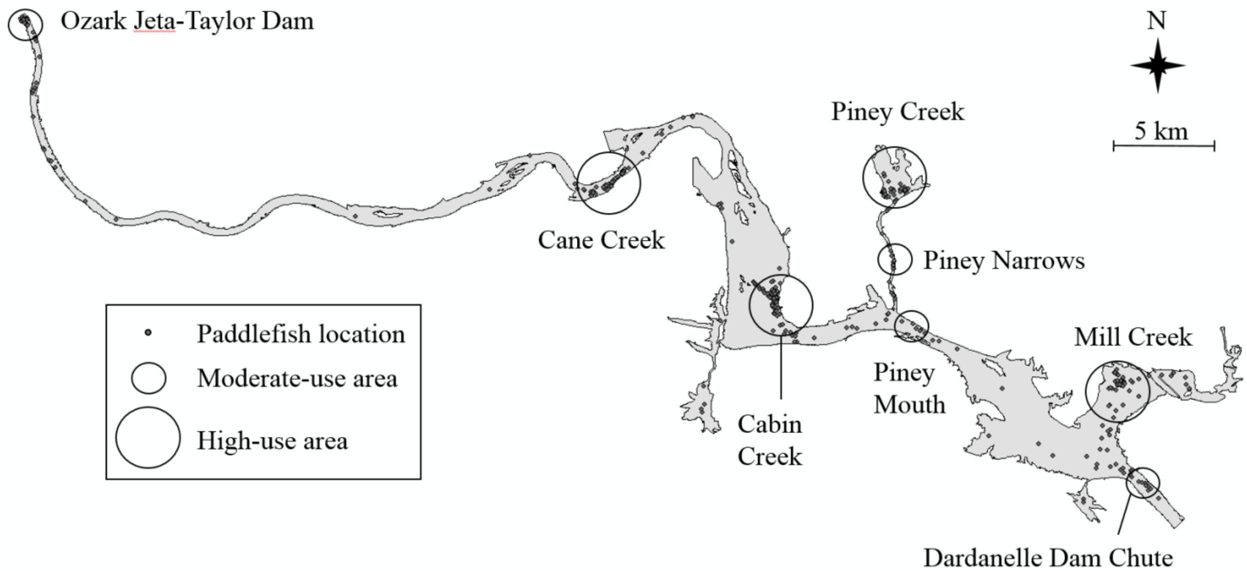

Figure 1.4: Individual paddlefish detections recorded from April 2014 through October 2015; high-use areas (≥10% of all detections); and moderate-use areas (4-10% of all detections).

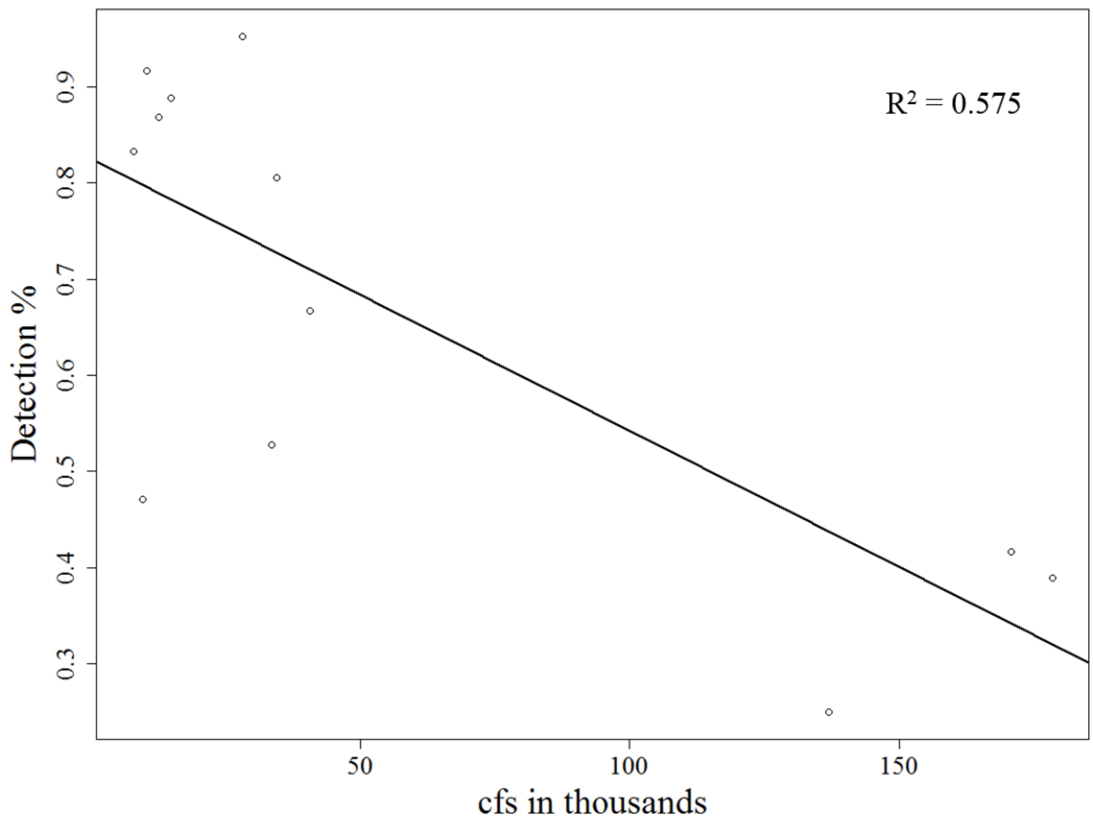

Figure 1.5: Relationship between paddlefish tracking detection percentage and flow (in thousands of cfs) in Lake Dardanelle, Arkansas.

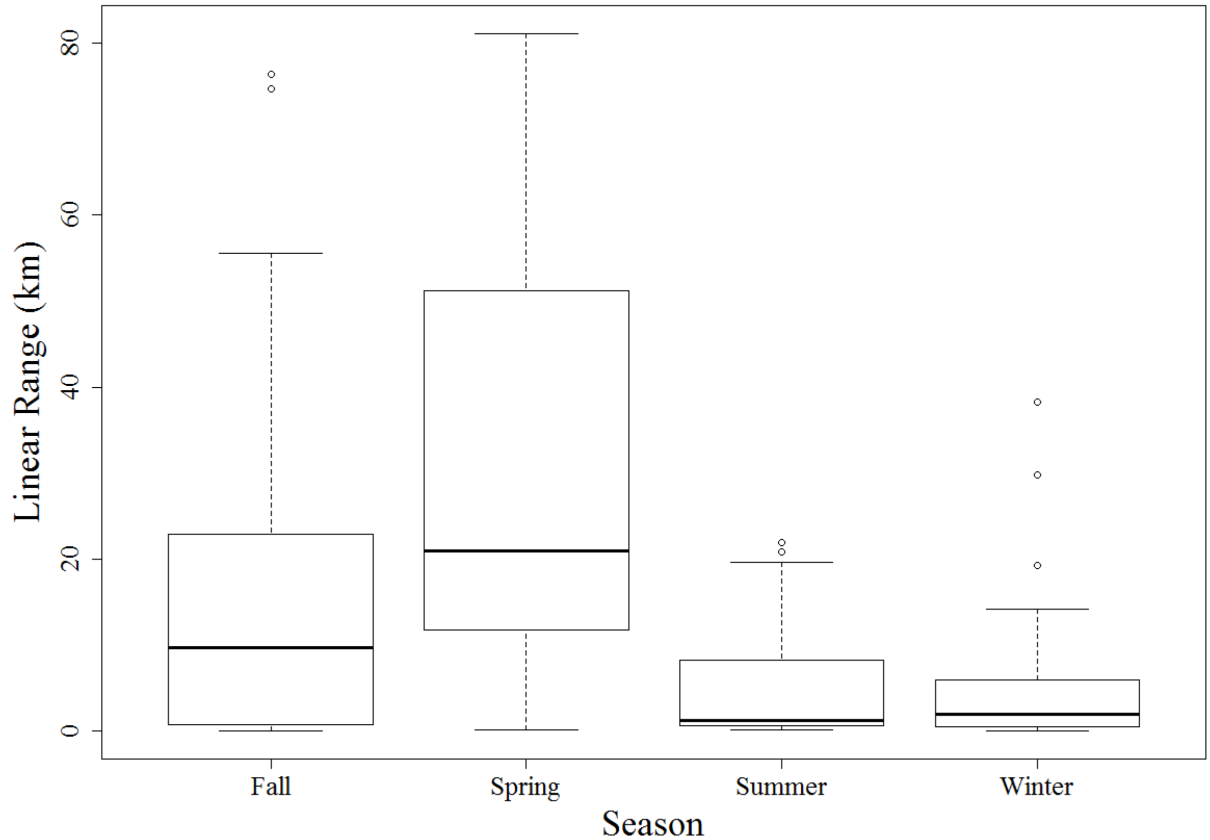

Figure 1.6: Seasonal linear range for paddlefish telemetered from October 2014 through September 2015 in Lake Dardanelle, Arkansas.

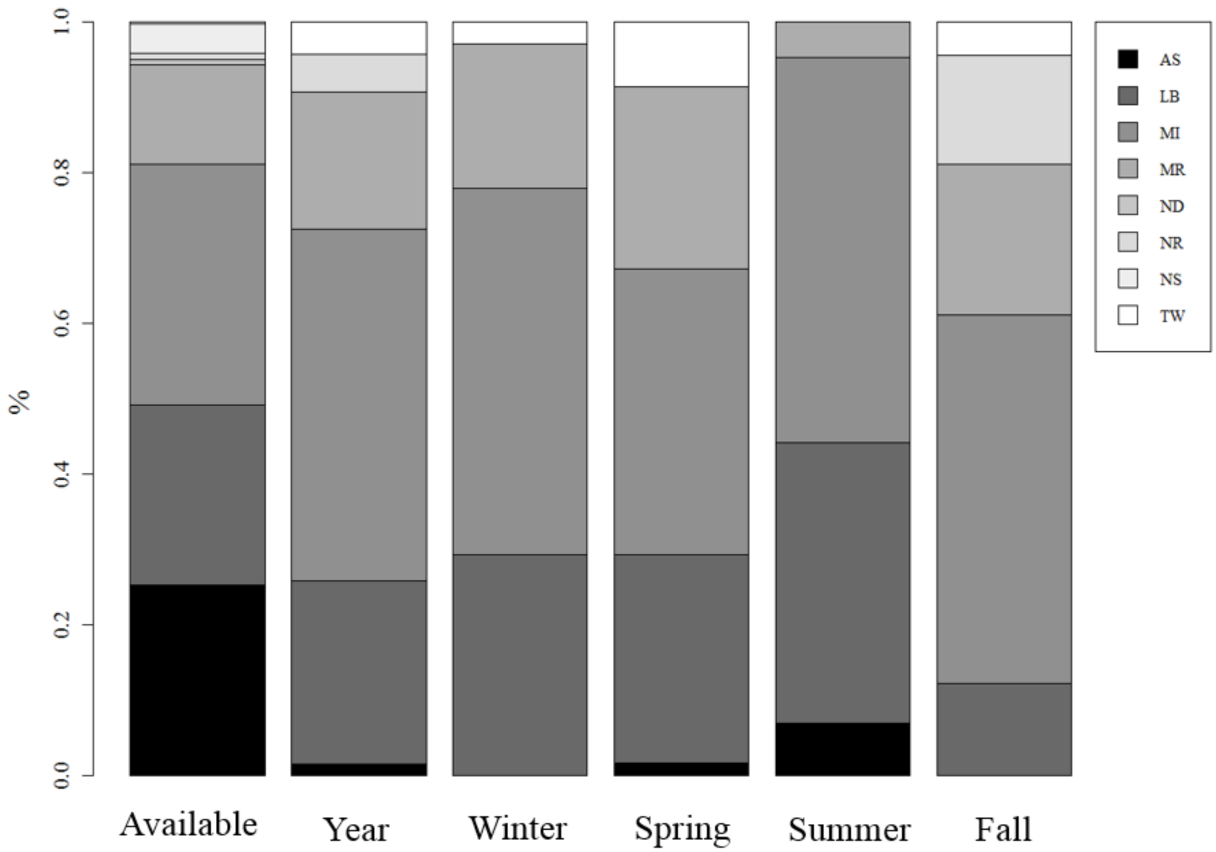

Figure 1.7: Paddlefish macrohabitat availability and selection for October 2014 through September 2015 in Lake Dardanelle, Arkansas. Refer to Table 1.1 for habitat abbreviations.

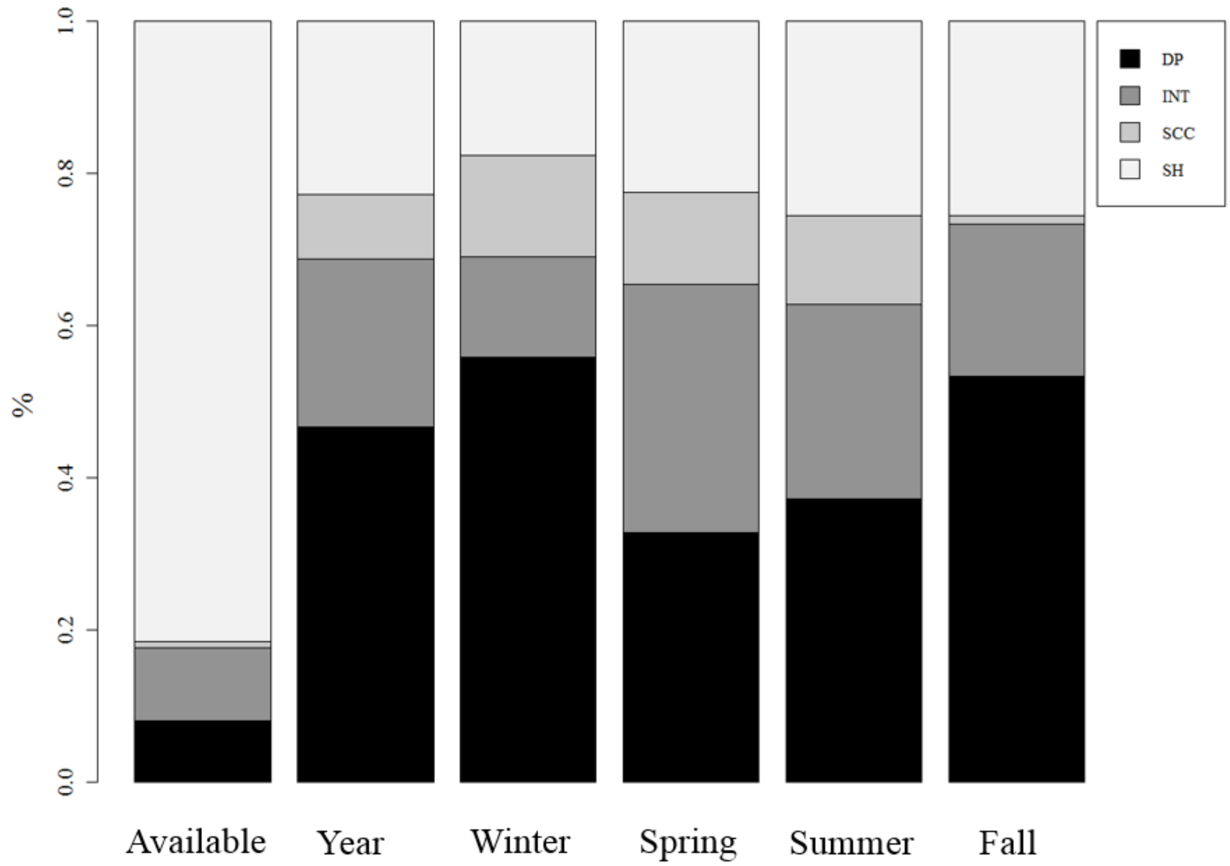

Figure 1.8: Paddlefish bathymetric habitat availability and selection for October 2014 through September 2015 in Lake Dardanelle, Arkansas. Refer to Table 1.2 for habitat abbreviations.

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APPENDIX

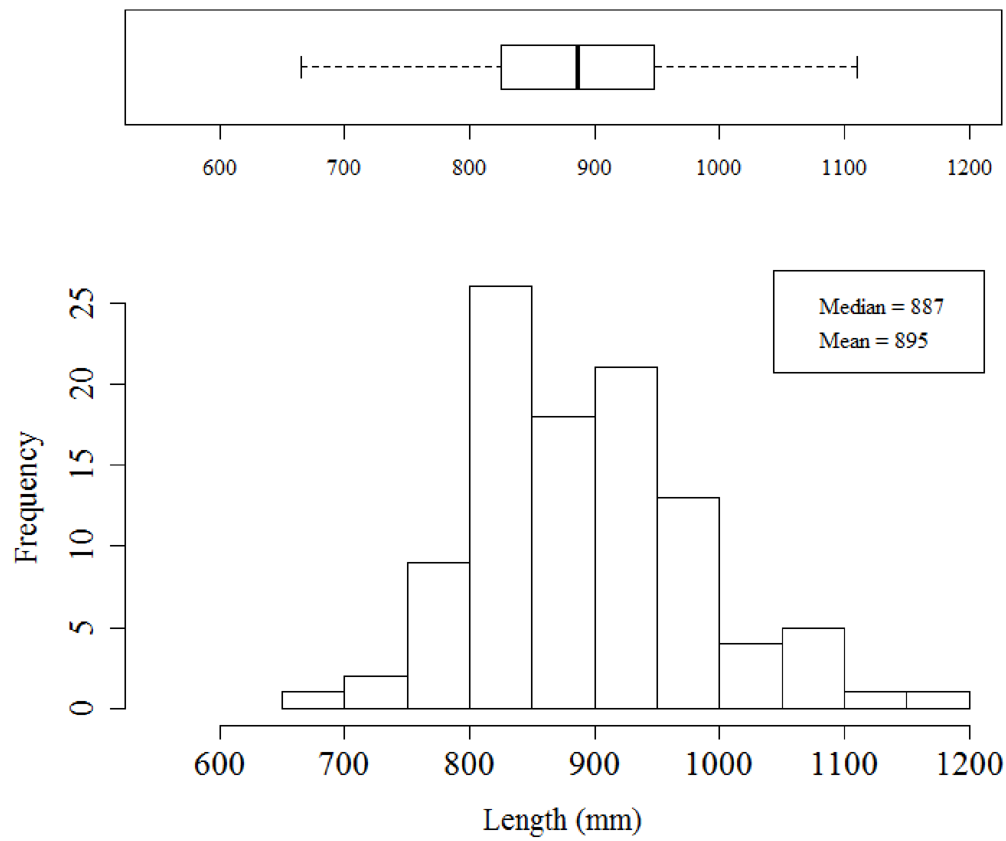
Lengths, capture locations, capture dates, and implantation status of every paddlefish captured during the study.

Fish	Length (mm)	Capture Location	Capture Date	Implanted with Transmitter
1	665	Cane Creek	4/12/2014	N
2	750	Cabin Creek	5/18/2014	N
3	750	Cane Creek	7/29/2014	Y
4	755	Piney Narrows	5/9/2014	N
5	770	Cane Creek	4/12/2014	N
6	785	Cane Creek	5/23/2014	Y
7	790	Cabin Creek	5/18/2014	Y
8	790	Cabin Creek	5/18/2014	Y
9	790	Cabin Creek	5/18/2014	Y
10	790	Piney Bay	6/17/2014	N
11	795	Piney Bay	6/17/2014	Y
12	800	Piney Bay	6/17/2014	Y
13	810	Cane Creek	4/12/2014	N
14	810	Cabin Creek	5/18/2014	Y
15	813	Cabin Creek	12/7/2014	N
16	815	Cabin Creek	5/17/2014	N
17	815	Piney Bay	6/17/2014	Y
18	816	Mill Creek	11/8/2014	N
19	820	Cabin Creek	5/17/2014	N
20	820	Cabin Creek	5/18/2014	Y
21	820	Cabin Creek	5/18/2014	N
22	820	Above Dardanelle Dam	5/25/2014	N
23	820	Piney Bay	6/17/2014	Y
24	824	Cabin Creek	12/7/2014	N
25	825	Piney Narrows	5/16/2014	N
26	825	Piney Bay	6/17/2014	Y
27	825	Piney Bay	6/17/2014	N
28	830	Cabin Creek	5/18/2014	Y
29	832	Mill Creek	11/8/2014	Y
30	835	Piney Narrows	5/16/2014	N
31	835	Piney Bay	6/17/2014	Y
32	835	Piney Bay	6/17/2014	N
33	840	Cabin Creek	5/17/2014	N
34	842	Cabin Creek	11/1/2014	Y
35	843	Mill Creek	11/6/2014	N
36	845	Mill Creek	6/10/2014	Y
37	846	Cabin Creek	11/7/2014	Y
38	850	Piney Bay	6/17/2014	N
39	855	Piney Bay	6/17/2014	N
40	860	Cabin Creek	5/17/2014	N
41	861	Cabin Creek	12/7/2014	N
42	870	Mill Creek	5/29/2014	Y
43	872	Cabin Creek	11/1/2014	Y
44	875	Cabin Creek	11/7/2014	Y
45	878	Cabin Creek	11/7/2014	Y
46	880	Above Dardanelle Dam	5/27/2014	N
47	880	Mill Creek	6/10/2014	Y
48	881	Cabin Creek	12/7/2014	N
49	885	Mill Creek	6/10/2014	Y

Fish	Length (mm)	Capture Location	Capture Date	Implanted with Transmitter
50	885	Piney Bay	6/17/2014	N
51	887	Mill Creek	11/6/2014	Y
52	887	Cabin Creek	12/7/2014	N
53	890	Cane Creek	4/12/2014	N
54	890	Mill Creek	6/10/2014	Y
55	890	Piney Bay	6/17/2014	N
56	895	Cabin Creek	12/7/2014	Y
57	901	Cabin Creek	11/7/2014	N
58	905	Cabin Creek	5/17/2014	N
59	905	Horsehead	6/30/2014	N
60	909	Cabin Creek	12/7/2014	N
61	910	Piney Bay	6/17/2014	Y
62	910	Piney Bay	6/17/2014	N
63	920	Cabin Creek	5/17/2014	N
64	920	Cabin Creek	5/18/2014	N
65	920	Mill Creek	6/10/2014	Y
66	925	Piney Bay	6/17/2014	N
67	927	Mill Creek	11/6/2014	Y
68	930	Above Dardanelle Dam	5/25/2014	N
69	934	Mill Creek	11/8/2014	N
70	935	Mill Creek	6/10/2014	Y
71	935	Piney Bay	6/17/2014	Y
72	936	Cabin Creek	12/7/2014	Y
73	942	Cabin Creek	11/1/2014	Y
74	944	Cabin Creek	11/1/2014	Y
75	947	Cabin Creek	11/7/2014	Y
76	948	Cabin Creek	11/7/2014	Y
77	950	Cabin Creek	5/17/2014	N
78	951	Cabin Creek	11/7/2014	Y
79	955	Piney Narrows	5/16/2014	Y
80	955	Piney Narrows	5/16/2014	N
81	955	Cabin Creek	12/7/2014	Y
82	959	Cabin Creek	11/7/2014	Y
83	967	Cabin Creek	12/7/2014	Y
84	968	Cabin Creek	11/1/2014	Y
85	970	Piney Bay	5/17/2014	N
86	975	Piney Bay	6/17/2014	N
87	980	Cabin Creek	11/1/2014	N
88	981	Cabin Creek	11/1/2014	Y
89	985	Piney Bay	6/17/2014	N
90	986	Cabin Creek	11/1/2014	Y
91	1004	Cabin Creek	11/7/2014	Y
92	1030	Horsehead	6/30/2014	Y
93	1034	Cabin Creek	11/1/2014	N
94	1035	Cabin Creek	5/17/2014	N
95	1054	Mill Creek	11/8/2014	Y
96	1060	Mill Creek	5/29/2014	N
97	1083	Cabin Creek	11/1/2014	Y
98	1091	Cabin Creek	11/1/2014	N
99	1100	Mill Creek	11/6/2014	Y
100	1110	Above Dardanelle Dam	5/26/2014	N
101	1181	Cabin Creek	11/7/2014	N

Monthly detection percentages for telemetered individual paddlefish. Letters and shading denote: not detected (dark gray shading), detected (x), captured for implantation but not detected otherwise (C), and commercially harvested (H). October 2014 – September 2015.

		Month											
ID	Detection Percentage	O	N	D	J	F	M	A	M	J	J	A	S
2	75%		x	x	x	x	x		x	x	x	x	
3	75%		x	x	x	x		x		x	x	x	x
4	50%		x	x	x	x	x	x					
5	42%		x		x	x	x	x					
6	33%		x	x		x	x						
7	50%		x	x	x	x	x	x					
9	50%		x	x	x	x	x	x					
10	58%	x	x	x		x	x	x		x			
11	58%	x	x	x	x	x					x		x
18	42%		C	x	x	x						x	x
26	67%		x	x		x	x	x	x			x	x
38	83%		x		x	x	x	x	x	x	x	x	x
41	83%	x	x	x	x	x	x	x	x			x	x
42	58%		x	x	x	x	x		x			x	
55	17%		x	x	H								
62	0%		C	H									
74	67%	x	x		x	x	x	x			x	x	
81	50%		x	x	x	x	x		x				
82	83%	x	x	x	x	x		x	x	x	x		x
88	92%	x	x	x	x	x	x	x		x	x	x	x
102	67%	x	x	x	x		x	x		x		x	
108	50%		x	x	x	x	x	x					
109	58%			x	x	x		x	x	x		x	
119	83%	x	x	x	x	x	x	x			x	x	x
122	58%	x	x	x	x	x	x	x					
123	25%	x	x	x	H								
128	83%	x	x	x	x	x	x	x	x	x		x	
144	75%	x	x	x	x	x	x	x				x	x
152	67%	x	x	x	x		x			x		x	x
174	75%	x		x	x	x	x	x	x	x			x
182	42%	x		x	x	x	x						
183	67%	x		x	x	x	x	x				x	x
190	50%	x		x	x	x						x	x
191	67%		x	x	x	x	x	x	x	x			
193	50%		C	x	x	x	x	x	x				
215	67%			C	x	x	x	x	x	x		x	x
301	58%	x	x	x	x	x	x		x				
302	17%	x	x										
303	92%	x	x	x	x	x	x		x	x	x	x	x
Available		21	36	38	36	36	36	36	36	36	36	36	34
Detected		20	30	33	32	33	29	24	15	14	9	19	16
Monthly Detection %		95%	83%	87%	89%	92%	81%	67%	42%	39%	25%	53%	47%



Length frequency of paddlefish implanted with a transmitter.