Spawning migration periodicity and river choice of the Grand Lake stock of Paddlefish *Polyodon spathula*

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Knowledge of movements, spawning, and reproductive periodicity of paddlefish (*Polyodon spathula*) is important for their successful management. Thirty gravid female Paddlefish were tagged with acoustic transmitters and their movements tracked in Grand Lake (a 21,000 ha impoundment) and in two tributaries, the Neosho River (NR) and Spring River (SR), northeastern Oklahoma, USA to assess their reproductive periodicity (annual versus non-annual) and their choice of river entered during their upriver spawning migration period (Feb 15 to May 15). Fish seldom occupied the rivers at other times and remained in the reservoir. Telemetered fish commonly used both rivers, with few using only one river each year and none using a single river exclusively over the four year study duration. Although annual spawning was the most common pattern, alternate-year spawning was observed. Over the four-year study, fish demonstrated a slight numerical preference for ascending the NR (96 times) over the SR (88 times), despite anomalously lower discharges in the NR. Results were not inconsistent with two other studies indicating the higher value of the NR over the SR as a paddlefish recruitment river. However, the lack of high flow years on the Neosho River during our study limited our interpretation. In testing hypotheses that pre-spawning fish would enter the river a) with the higher discharge on that day or within four days prior, b) with the greater increase (or lesser decrease) in discharge on that day or within four days prior, none of nine discharge variables investigated were closely related to river choice. Despite some specific instances where high or rising discharge each triggered upriver movements, river choice over the entire Feb 15 to May 15 period as a whole was similar to what would be expected by chance. Entering and exiting the two proximal, low gradient river mouths and lower river sections may have incurred little energetic cost prior to actual spawning.

Key words: Polyodontidae, fish migration, spawning, Oklahoma, Neosho River

INTRODUCTION

Effective management of paddlefish (*Polyodon spathula*), an ancient river-spawning species native to the central United States (Gengerke 1986; Bettoli, Kerns, and Scholten 2009), is predicated on understanding the reproduction and patterns of movements of this highly mobile, migratory species (Russell 1986; Jennings and Zigler 2000; Scarnecchia et al. 2007). Many aspects of the species' upriver spawning migrations and reproductive success

are influenced by interannual variations in riverine habitat quantity and quality (Braaten, Fuller, and Lott 2009; Schooley and Neely 2018; Tripp, Neely, and Hoxmeier 2019). Interannual variations in river conditions also influence less directed, non-spawning movements of stocks (Southall and Hubert 1984; Moen, Scarnecchia, and Ramsey 1992; Tripp, Neely, and Hoxmeier 2019). These variations may include differing seasonal discharge, magnitude, as well as timing, turbidity, and water temperatures. When

alternative rivers are accessible to migratory fish of a particular stock, (i.e. river choice is possible) river discharge, turbidity, water temperatures, and other factors can, in some instances, also affect the specific choice of one or another river for migration and for spawning (Firehammer, Scarnecchia, and Ryckman 2001). River fidelity may be another factor influencing river choice in this species (Braaten, Fuller, and Lott 2009).

The stock of paddlefish inhabiting Grand Lake O' the Cherokees, Oklahoma (hereafter Grand Lake) provides the state's most important and popular recreational (snag) paddlefish fishery (Schooley, Scarnecchia, and Crews 2014). Paddlefish in Grand Lake, as in other localities, make pre-spawning movements and spawn in spring associated with higher discharges, often

associated with greater inundation of spawning gravels (Russell 1986; Miller, Scarnecchia, and Fain 2011; Schooley and Neely 2018). Reproductive periodicity of individual fish had, until recently been undocumented, although the high metabolism of this southerly stock would suggest that annual spawning by females would occur as opposed to a two- or three-year spawning cycle commonly seen farther north (Meyer 1960; Scarnecchia et al. 2007, 2011). In addition, choice of river during spring upstream migrations from the reservoir into the Neosho River (hereafter NR) or Spring River (hereafter SR), the two main rivers entering Grand Lake within a kilometer of each other (Fig. 1), is not well documented.

Telemetry, either acoustic or radio, has proven useful in numerous situations for assessing paddlefish migrations (Firehammer and Scarnecchia 2006), short term movements, habitat use (Southall and Hubert 1984; Moen, Scarnecchia, and Ramsey 1992), and spawning periodicity (Miller and Scarnecchia 2011). Studies on paddlefish movements have been conducted outside of Oklahoma on both juveniles (Barry et al. 2007; Pitman and Parks 2004; Roush, Paukert, and Stancill 2003) and adults (Southall and Hubert 1984; Zigler, Dewey, and Knights 1999; Firehammer and Scarnecchia 2006). Within Oklahoma, acoustic telemetry studies on paddlefish have been conducted in Grand Lake (Johnston and Gordon 2010), on the NR and SR (ODWC, unpublished data), and elsewhere in the state (Paukert and Fisher 2000; Patterson 2009). Monitoring movements of individual fish over a series of years can provide insight into sex-specific reproductive periodicity. It can also provide information on factors affecting spawning migrations and river choice in relation to habitat conditions, especially river discharge and its changes.

This paper focuses on two aspects of a four-year telemetry project on Grand Lake (Schooley and Johnston 2012; 2013; 2014; and 2015): reproductive periodicity and river choice (i.e. the NR or SR) by pre-spawning female paddlefish in spring. For reproductive periodicity, we hypothesized that spawning, as indicated by spring migratory movements
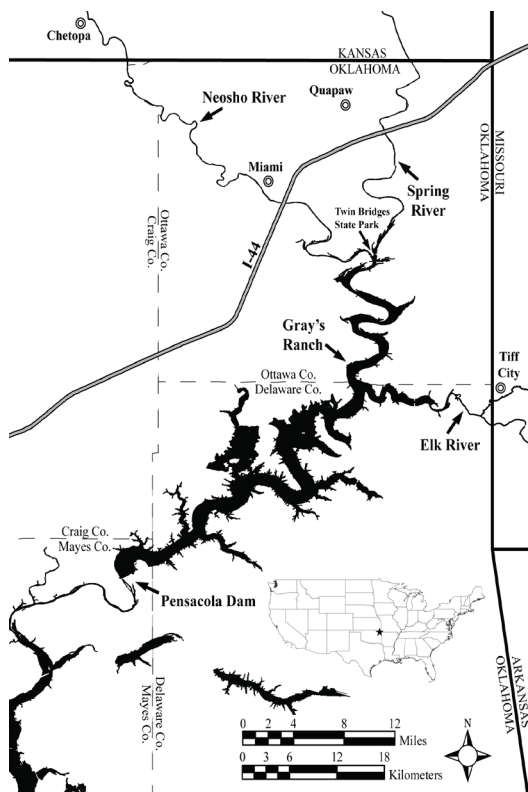
Figure 1. Map of Grand Lake O' the Cherokees, Northeast Oklahoma, with its primary tributaries- the Neosho and Spring rivers, which are valuable for Paddlefish spawning.

from feeding locations in the reservoir into the rivers, would typically occur annually, as opposed to a two- or three-year spawning interval (Firehammer and Scarnecchia 2006; Scarnecchia et al. 2007), consistent with the high metabolic rate of the Grand Lake stock (Scarnecchia et al. 2011) and other southern stocks (Lein and DeVries 1998; Scholten and Bettoli 2005). For river choice, our first hypothesis was that pre-spawning fish staging in spring below at the Grand Lake headwaters, their choice and entry into one or the other river (NR or SR) as detected in a given day D would be preferentially into the river a) with the highest discharge on that day or within four days prior, b) with the greatest increase (or lesser decrease) in discharge on that day or within four days prior. Alternative hypotheses would be that this river choice would not be directed primarily by discharge conditions, but may be random, or be directed by fidelity to a particular river or be made by cueing on other habitat features besides discharge such as substrate, turbidities, water temperatures, or other unidentified factors (Mettee, O'Neil, and Rider 2009). Addressing these hypotheses has relevance not only to the Grand Lake stock, but to understanding and anticipating how life histories and movements of paddlefish affect spawning success and the location of fisheries.

Materials and Methods

Study site: The study site included Grand Lake, a 21,000 ha impoundment and its two main inflowing tributaries, the Neosho River (NR) and Spring River (SR) draining the humid-continental tri-state region of northeast Oklahoma, southeast Kansas and southwest Missouri (Fig. 1). The study was focused within the Oklahoma portion of this region, the area most accessible and most occupied by the Grand Lake stock of paddlefish. Grand Lake provides the primary rearing habitat for the stock.

The two main inflowing rivers, NR and SR, which flow into Grand Lake within a half kilometer of each other at Twin Bridges State Park (Fig. 1), have different origins and characteristics. The NR rises in the Flint Hills Region of Morris County, Kansas where a dam at Council Grove forms its first

impoundment, Council Grove Lake (1,309 ha; completed 1960), The Cottonwood River from the south merges with the Upper Neosho River above where a second dam forms John Redmond Reservoir near New Strawn (3,271 ha; completed 1964). The NR then flows southeasterly through the towns of Iola, Oswego, and Chetopa, Kansas (site of a low-head dam and a spring fishery; Scarnecchia et al. 2013; Neely, Pracheil, and Lynott 2014), entering Oklahoma in Craig County and continuing its southeasterly course through Miami, Oklahoma, site of another low-head dam and fishery (Gordon 2009), and into Grand Lake at Twin Bridges State Park. Most of the watershed in Kansas and Oklahoma is within the Osage Plains section of the Central lowlands. Land use in this primarily rural area is dominated by livestock grazing and row-crop agriculture (Marcher et al. 1984). With the SR now flowing into Grand Lake, about 6 % of the NR watershed (minus the SR) is in Oklahoma.

The natural discharge in the NR is strongly driven by precipitation in the form of rain. According to Marcher et al. (1984), "*A large percentage of rainfall occurs during short, intense thunderstorms associated with squall lines ahead of frontal systems during spring and summer; about 75% of the annual precipitation falls during this period.*" (p. 30). Discharges are typically highest during this period; mean discharge is typically highest in June (mean, 196 m³/sec), followed by May (mean, 182 m³/sec) and April (mean, 155 m³/sec; http://waterdata.usgs.gov/nwis/uv?07185000, although heavy rains in other season can also result in high discharges and severe flooding (e.g., the major flood of 1986; The Miami Kiwanis Club, nd). These rains, along with water releases from John Redmond Reservoir, drive hydrograph increases in spring that have long been recognized by biologists and anglers to induce upriver movements of paddlefish from Grand Lake to Miami (Gordon 2009; Scarnecchia et al. 2013) and Chetopa, Kansas and increase their vulnerability to snag fisheries (Scarnecchia et al. 2013, their Fig. 3; Neely, Pracheil, and Lynott 2014). Flood stage for the NR at Commerce is 4.57 m (NWS 2014a). During spring flood periods, the river is characterized by highly turbid, debris-laden

waters that commonly flood low-lying areas along the banks. Schooley and Neely (2018) identified the NR as having more prolonged periods of flood stages than the SR.

The 208 km long SR arises in Barry County, Missouri, flows westward before crossing into Cherokee County, Kansas, south into Ottawa County, Oklahoma, and then into Grand Lake immediately to the east of the NR inflow into Grand Lake (Fig. 1). The name "Spring River" derives from a number of springs and seeps which provide baseflow. The Spring River has less than half the watershed area (i.e. 42 %; watershed area at Twin Bridges = 6,677 km^2) compared to the Neosho River (watershed area at Twin Bridges = 15,871 km^2), so it is a much smaller system. However, the Spring River receives more rainfall, has more groundwater, and has no large storage reservoirs, which helps prevent there from being as much of a discrepancy in discharge between the two river systems as would be anticipated based on watershed area.

As a spring-fed river, SR variations in mean monthly flow are more stable than in the NR. Mean monthly discharges are within 80% of NR discharges during the low flow months of December and January, but the SR discharges only about half as much water on average as the Neosho during the peak months of May and June (Fig. 2). Flood stage for the SR at Quapaw is 6.10 m (NWS 2014b). The SR has less
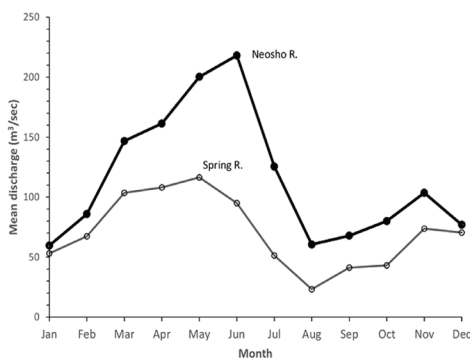

Figure 2. Mean of mean monthly discharges for Neosho River near Commerce, Oklahoma (USGS 07185000; 1970-2015) and Spring River near Quapaw, Oklahoma (USGS 07188000; 1970-2015).

prolonged flood peaks than the NR (Schooley and Neely 2018). Like the NR watershed, the SR watershed has heavy agricultural use; water quality has been impacted by high concentrations of phosphorus and nitrates (Chambers, Arruda, and Jaywardhana 2005). In spring, the SR is typically less turbid and less debris-laden than the NR. Both rivers, however, and especially the SR as well as Grand Lake, continue to be impacted by past widespread lead and zinc mining in the tri-state region (Weidman 1931; Gibson 1972; U.S. EPA 2000; Juracek and Becker 2009; Manders and Aber 2014). Starting in 2010, the SR was closed to snagging; the NR has remained open to paddlefish harvest year-round (Schooley, Scarnecchia, and Crews 2014).

Study fish: Paddlefish were captured near Gray's Ranch (Fig. 1) on Grand Lake on January 24 and 25, 2011, with monofilament gill nets (91.4 m x 7.3 m x 15.2 cm mesh). Captured fish were immediately evaluated to determine sex and maturation state. Those fish not able to be eliminated by size or shape as mature females were administered a small incision; blunt scissors were used to puncture the peritoneal cavity and presence of mature roe was visually determined for each fish. Netted fish determined to not be gravid had their small incision sutured and were released immediately.

Thirty gravid female paddlefish were selected for tagging. Body lengths (front of eye to fork of caudal fin) of tagged fish ranged from 1,014 to 1,138 mm; weights ranged from 17.30 to 24.70 kg. All tagged fish had Stage 4 (caviar-quality) eggs (three with green-colored roe, one with gold-colored roe, and 26 with the most common, grey-colored roe). Each female fish selected for telemetry was also tagged with uniquely-coded aluminum monel bands on the left side of the lower jaw. Bands were painted bright orange for ease of identification from other jaw tagged but non-telemetered fish.

Surgical implantation of tags: Each fish was surgically implanted with an ultrasonic transmitter. Fifteen transmitters were Sonotronics® DT-97-L and fifteen were Sonotronics® CTT-83-3-I. All tags were tuned to a 70 sec ping interval to extend the life to

an estimated 48 months. Surgical procedures for tag implantation were similar to those described in Johnston and Gordon (2010) and were performed with the guidance of Dr. Gene Parker, Oklahoma State University College of Veterinary Medicine. After sterilization of transmitter, instruments, and surgical site with betadine and chlorhexidine, a 2.5 cm incision was made on the right side of the abdomen below midline. The transmitter was manually inserted ventrally into the abdomen. The incision was closed with a PDS absorbable/phagocytic suture with two horizontal mattress sutures. Prior to implantation, each transmitter was tested for functionality. All fish were immediately released after surgery near Gray's Ranch, and passive monitoring commenced upon release.

Tracking and monitoring system: Data for this study relied on submersible ultrasonic receivers (SUR) strategically deployed using concrete anchors throughout Grand Lake and the NR and SR in order to maximize coverage. Over the duration of the project, SUR locations varied based on successes and failures, however basic coverage was maintained. River stations were chosen based on accessibility and prior knowledge of spawning locations while providing adequate coverage to discern transitional movements between reservoir and river(s). Placement of SUR stations is thoroughly described in Schooley and Johnston (2015).

Fish tracking: Tag detections were summarized by fish, transmitter type, and SUR. SUR data were downloaded directly to a tethered laptop computer and checked for errors via Sonotronics® software SURSoft and SUR Data Processing Center (DPC). Data were auto-processed (telemetry-matched) in DPC in batches of two or more raw files. Processed files were consolidated into a master datasheet in Microsoft Excel and linked to a Microsoft Access database for analysis. DPC contained filtering mechanisms to remove erroneous detections, yet due to colliding acoustic signals, some detection errors remained. Therefore, processed data were secondarily filtered for non sequitur values and other errors. These filtering mechanisms were not interpretive of context, therefore orphan detections (which are

typically errors) remained. It therefore became necessary to establish objective criteria for defining an "active" fish. Only fish with 100 or more detections in a calendar year were considered active (Schooley and Johnston 2015). Fish detected at one or more river SUR stations were presumed to be attempting a spawning migration. Other studies (e.g., Miller and Scarnecchia 2008) and the scarcity of spawned-out fish caught in the rivers in spring have indicated that spawned-out fish typically exit rivers soon after spawning for more productive feeding areas in reservoirs.

Validated fish records: Over the period 2011-2014, thousands of validated records were obtained from the SUR locations. Twenty-nine of the 30 tagged females provided records in 2011 and were detected on a regular basis. Total detections during 2012 – 2014 were substantially fewer. Many fish with thousands of detections in 2011 were only detected tens of times in 2012. Because of the small sample size in 2014, the river choice hypotheses were evaluated using fish from only 2011, 2012 and 2013. Additional details of data validation and ground-truthing using test transmitters are described in Schooley and Johnston (2015).

Hypotheses: For spawning periodicity, we assumed that pre-staging and entry into the rivers in spring was indicative of an attempted spawning event that year. Support for this assumption comes from harvest data indicating that nearly all adult female fish harvested in the NR (as opposed to Grand Lake) over the study period had Stage 4 eggs that could be spawned in that spring period, indicating that nearly all mature females ascending the rivers do so to spawn. Absence of a validated record in the river for a year (followed by valid records in Grand Lake later in the year) would indicate reservoir residency that year and non-annual spawning.

River choice over the period 2011-2013 was assessed by evaluating validated records from reservoir and river SUR stations for each at-large fish. River selection was identified for 2014 in this paper but not statistically analyzed because of the few fishes at-large (n = 4). For 2011-2013, we used a specific subset of the data, over the period February 15 to May 15,

when a fish moved from any reservoir station (based on detections) to a river station in one or the other river (based on detections), the day of detection in the river designated as day D. It was hypothesized that for fish staging at Twin Bridges State Park and below, river choice would be related to their absolute discharges and changes in discharge in each river. Discharge data were obtained from the Neosho River near Commerce, Oklahoma (USGS 2015a [07185000]) and the Spring River near Quapaw, Oklahoma (USGS 2015b [07188000]). These differences in discharge and changes in discharge were investigated for decision day D and for the 4-day period immediately prior to the decision day. This approach was designed to assess if there was a lag between discharges and fish movements. The nine discharge variables investigated in the NR and SR in relation to individual river choice decisions were:

Daily mean discharges (Q) expressed in a total of five ways:
Q(D) = Daily mean discharge in cubic meters per second (m^3/sec) on the date "D"
Q(D-1) = Daily mean discharge in m^3/sec on the date "D-1"
Q(D-2) = Daily mean discharge in m^3/sec on the date "D-2"
Q(D-3) = Daily mean discharge in m^3/sec on the date "D-3"
Q(D-4) = Daily mean discharge in m^3/sec on the date "D-4"

and discharge differences expressed in a total of four ways:
Q(D) - Q(D-1)
Q(D) - Q(D-2)
Q(D) - Q(D-3)
Q(D) - Q(D-4)

Over the three-year period, each reservoir to river choice as identified on day D was matched with the nine discharge variables for each river (NR and SR), and a determination was made whether a fish responded to the greater discharge as opposed to a lesser discharge, or a greater change in discharge (positive or negative, not absolute value), as opposed to a lesser change in discharge (positive or negative, not absolute value), and which river was chosen.

Plots of river choice over the period 2011-2013 versus the nine discharge variables were compared statistically to assess how a decision to enter the NR or SR was associated with concurrent discharges of the two rivers. In addition, for the obtained sample of two categories (e.g., more/less), a one sample binomial test was performed using PROC FREQ in SAS. The normal approximation method was used to test hypothesis of random paddlefish movement from reservoir to either river (i.e. $H_o = 0.5$ versus $H_o \neq 0.5$; two-tailed, non-directional test with test statistic

$$z = \frac{(\hat{p} - p_0)}{\sqrt{\dfrac{p_0 (1 - p_0)}{n}}}$$

$\hat{p}$ = sample proportion
p_0 = hypothesized population proportion
n = sample size

RESULTS

Spawning migration periodicity: The overall pattern of seasonal movements of paddlefish between reservoir and river occupancy was similar during each of the four years. Females seldom used the rivers other than during the spring migration period, consistent with the *a priori* designation of Feb 15 to May 15 as the probable window of river occupancy for spawning. During 2011, 26 of 29 active fish entered and occupied one or both rivers (i.e. at least three detections) at some time during the year. Most fish (17 of 26) used both rivers, six entered only the NR and three fish used only the SR. In 2012, 8 of 15 active fish used one or both rivers (i.e. at least three detections); seven fish used both rivers and one fish used only the SR. Those eight fish were confirmed by numerous detections to have migrated into the NR or SR the previous year. Seven active fish were not observed in the rivers in 2012. In 2013, all 10 active fish used one or both rivers; seven fish used both rivers, two fish used only the NR, and one fish used only the SR. Six of the 10 fish had been detected in one or both rivers in three consecutive years. The other four fish were detected in the rivers in 2011, but not in 2012. In 2014, three of the four remaining active fish used both rivers; the other fish was

detected at the confluence of the NR and SR before retreating down into the reservoir. All four of these fish were consistently detected in the rivers (or, in one case, at the river mouths) in each of the four years.

River choice: Over the four-year study, fish chose the NR 96 times and the SR 88 times. Results from the four years were not consistent, however. In 2011, fish chose the NR 52 times and the SR 36 times. In contrast, in 2012 and 2013, fish chose the SR more frequently than the NR (2012: 13 SR vs. 10 NR; 2013: 34 SR vs. 29 NR). The NR and SR were chosen the same number of times (5 each) in 2014.

As is typical in most large rivers, discharge conditions in the two rivers over the study period Feb 15 to May 15 varied widely over the four years of the study. In 2011, both the NR and SR experienced repeated minor river surges and retreats between 85 and 283 m³/sec with only one day in the NR briefly reaching 453 m³/sec on February 26. Three of these minor events exceeded 283 m³/sec in the NR, though the SR only reached 226 m³/sec. This period of river stage fluctuation spanned more than 60 days before both rivers crested on April 26. The year 2011 had the greatest number of individual fish making river choices.

Discharges were typically higher in the NR until March 27, during which time more fish chose the NR. After March 27, discharges were higher in the SR than in the NR, in stark contrast to long term trends (Fig. 3) and the fish tended to choose both rivers in similar proportions. After April 9, SR discharges always exceeded those in the NR; however, large numbers of fishes continued to choose the NR (Fig. 4). Overall, the NR was often chosen whether or not NR discharges exceeded those of the SR, whereas SR tended to be chosen only when its discharges were higher or comparable to those of the NR. This pattern held for the lagged discharges (D-1 through D-4) as well (e.g., Fig. 5).

In 2012, discharges during the migration season were often much lower than in 2011, although they were punctuated by two extreme and more prolonged high-water events. By March 23, NR discharge had risen from 45 m³/sec to 1,115 m³/sec over the course of four days (a 2,463% increase) and receded to low levels in another two days (Fig. 3). The rise in the SR occurred much more rapidly, from 18 m³/sec to 801 m³/sec over two days (a 4,354% increase). The first major high-water event in 2012 occurred one month earlier than in 2011. The second high water event of 2012 (May 2)
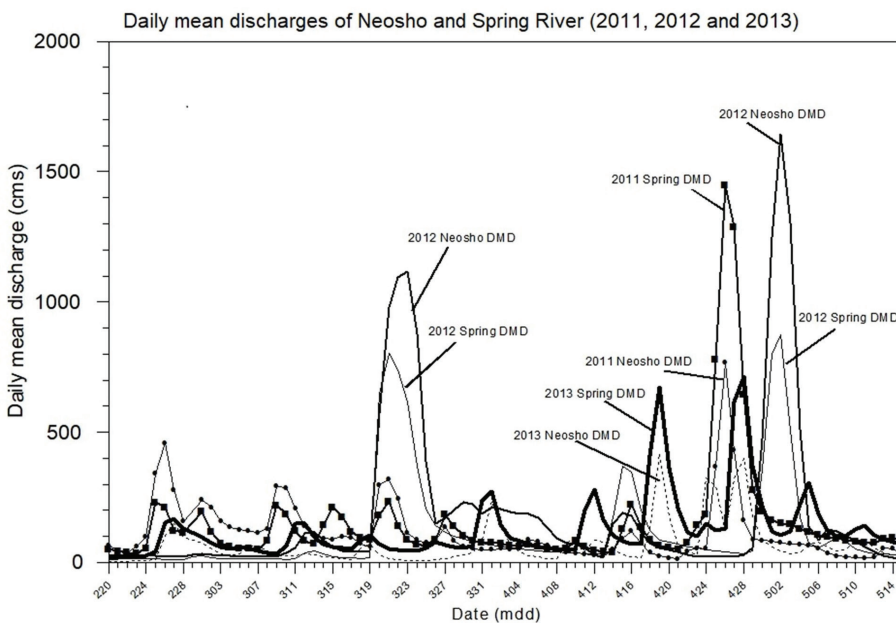

Figure 3. Daily Mean discharges of the Neosho River near Commerce, Oklahoma (USGS 07185000) and the Spring River near Quapaw, Oklahoma (USGS 07188000), February 15-May 15, 2011-2013.
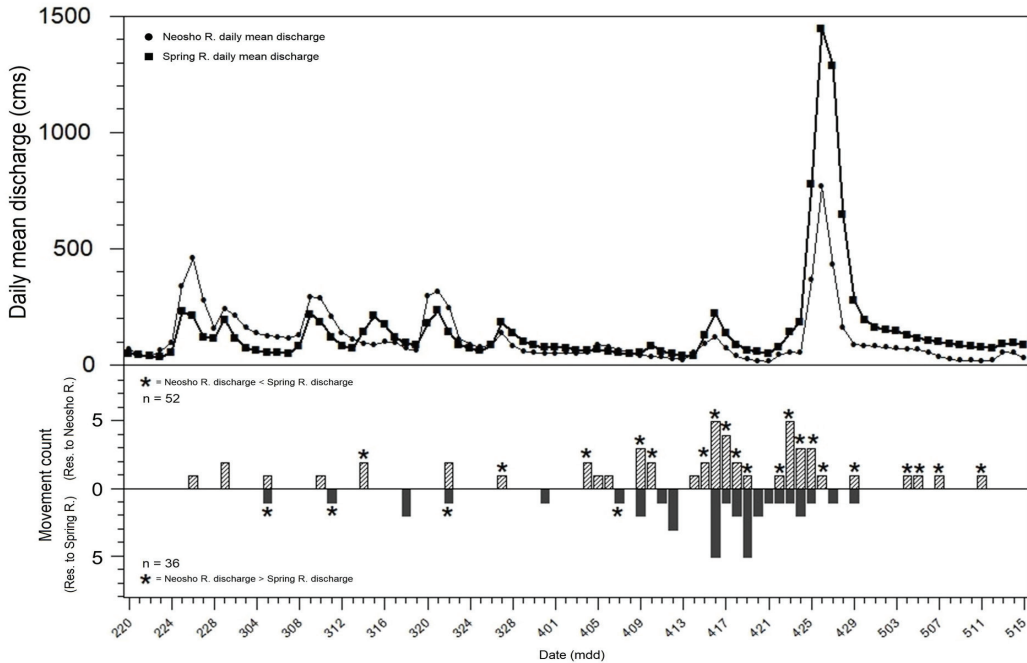
Figure 4. Number of choices of river (Neosho or Spring) in relation to daily mean discharge, Feb 15-May 15, 2011. No fish moved into rivers from Feb 15 through Feb 19. Asterisk (*) indicates choice of river with the highest discharge.
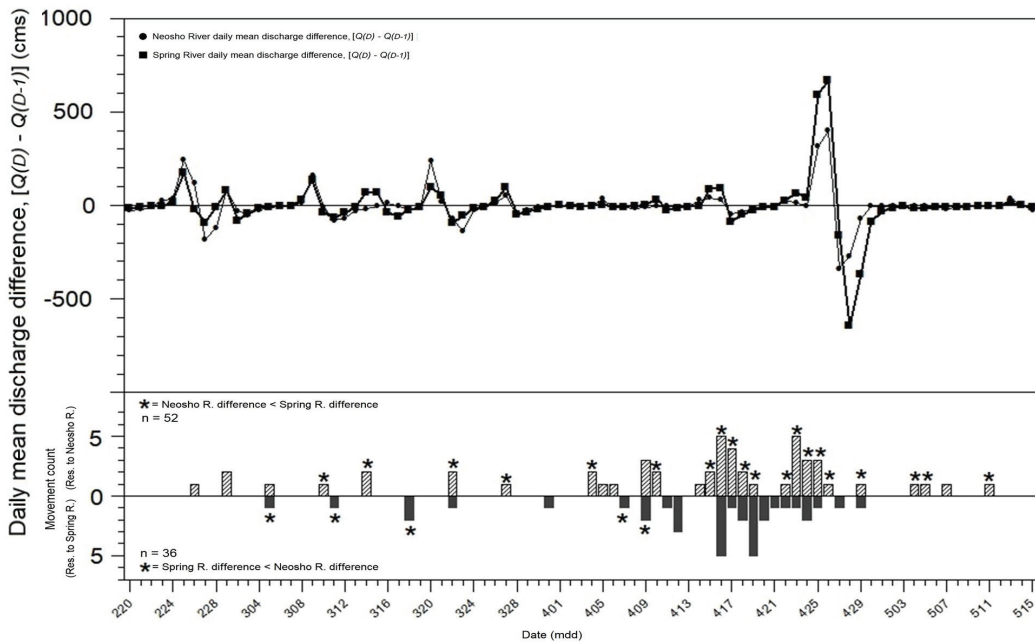

Figure 5. Number of choices of river (Neosho or Spring) in relation to change in change in discharge from the previous day, Feb 15 to May 15, 2011. No fish moved into rivers from Feb 15 through Feb 19. Asterisk (*) indicates choice of river with the highest change in discharge.

occurred approximately synchronous with the first event of 2011. This river cresting event was similar to the first one in the SR, but with much more magnitude in the NR, reaching 1,641 m³/sec (Fig. 3). In contrast to 2011, both 2012 cresting events demonstrated higher discharge in the NR than in the SR. During the first crest of the NR and SR in March, only three river choices were found, two into the NR and one into the SR. During the second crest in early May, following more than a month of low discharges in both rivers, no telemetered fish moved from reservoir to river, i.e. no fish chose one river over the other. Patterns with a 2-day lag in response were similar.

In 2013, neither river reached flood stage within the Feb 15 to May 15 study period. Contrary to long-term trends (Fig. 2), discharges in the SR exceeded those of the NR throughout most of the migration season, except for two brief (2-day) periods in April (Fig. 3). Although fish chose the SR (34 times) preferentially over the NR (29) times. Fish chose both rivers throughout the season (Figs. 6,7).

In 2014, as in 2013, the NR and SR remained at drought levels, well within their banks over the study period and throughout summer. Discharges exceeded 283 m³/sec for five days in the NR and two days in the SR (Fig. 3). Five choices each were made for the SR the NR.

Overall, none of the nine discharge variables were closely related to river choice. For daily mean discharges on days D, D-1, D-2, D-3 and D-4 over the 3-year period 2011-2013, none of 15 comparisons showed a statistically significant relationship with river choice (Table 1). For discharge differences, in only two of 15 comparisons showed a statistically significant relationship with river choice: discharge differences between D and D-2 in 2013 ($p = 0.0111$ and D and D-3 in 2013 ($p = 0.0226$; Table 2). Despite specific patterns outlined above, when examined over the entire migration season, results were similar to what would be expected by chance, i.e. if river choice were not driven by discharge.

DISCUSSION

Spawning migration periodicity: In this study, telemetered female Grand Lake paddlefish made annual spawning migrations in most, although not all, cases. This tendency toward annual spawning migrations is consistent with the ideas previously presented in the paddlefish life history framework (Scarnecchia et al. 2007) and with the metabolic theory of ecology (Scarnecchia et al. 2011). Fish with more compressed life histories associated with higher metabolic demands in southerly localities such as Oklahoma are expected to show a shorter period of gonadal recrudescence (i.e. annual spawning) than fish from more northerly stocks (i.e. non-annual spawning; Scarnecchia 2011). Russell (1986) summarized reports of spawning intervals and identified spawning intervals of two or more years in paddlefish from more northerly latitudes. In Montana's Yellowstone-Sakakawea stock, upriver migrations of younger mature female paddlefish peaked at three-year intervals, and almost no fish were found in rivers the year after tagging (Scarnecchia et al. 2007). Older age, prime female spawners in North Dakota seldom made spawning migrations in successive years, but typically migrated in alternate years, as in the Fort Peck stock of the Upper Missouri River (Scarnecchia et al. 2007; 2021). Unlike northern stocks of paddlefish with long lifespans, late-onset maturity, and spawning periodicity (two or three years), paddlefish in Grand Lake mature earlier, have shorter lifespans, put more energy into each spawn (higher Gonadosomatic Index (GSI) ; Scarnecchia et al. 2011; 2022) and are typically capable of spawning annually. Reproductive maturity for females is typically reached at 8-9 years with prime reproduction occurring between years 12 and 16, with relatively few fish living past 25-30 years (Scarnecchia et al. 2011). Under a higher metabolic demand in the southern areas, consecutive year spawning migrations in Grand Lake would maximize the reproductive potential of females in the population. Grand Lake female paddlefish, with their primarily annual spawning, are nearly all sexually mature females when they enter the NR and SR in spring (Oklahoma Department of Wildlife Conservation, unpublished data).
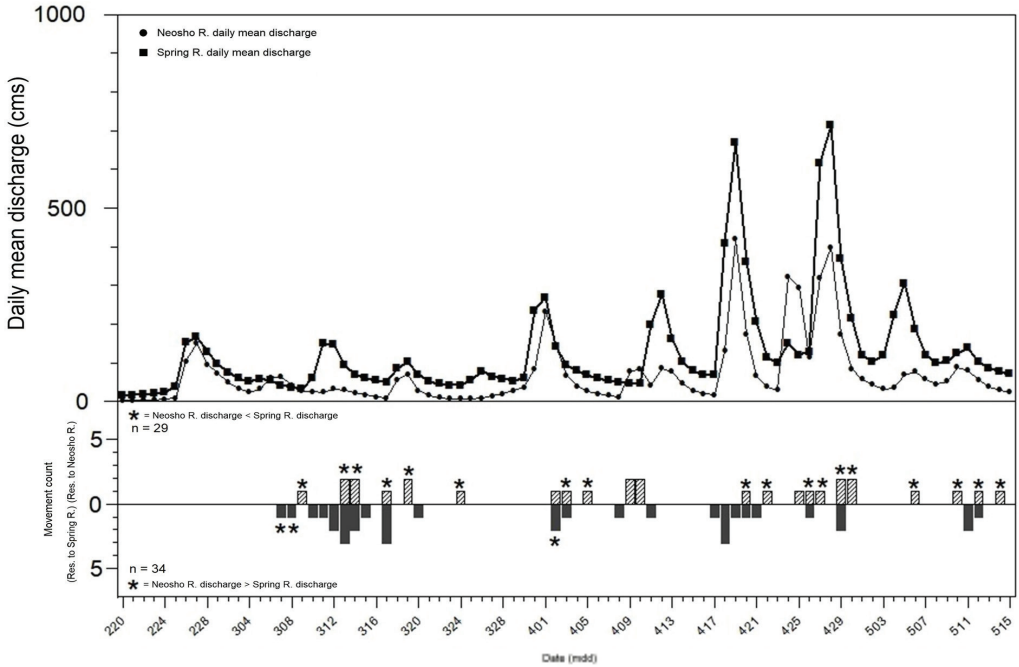
Figure 6. Number of choices of river (Neosho or Spring) in relation to daily mean discharge, Feb 15-May 15, 2013. No fish moved into rivers from Feb 15 through Feb 19. Asterisk (*) indicates choice of river with the highest discharge.
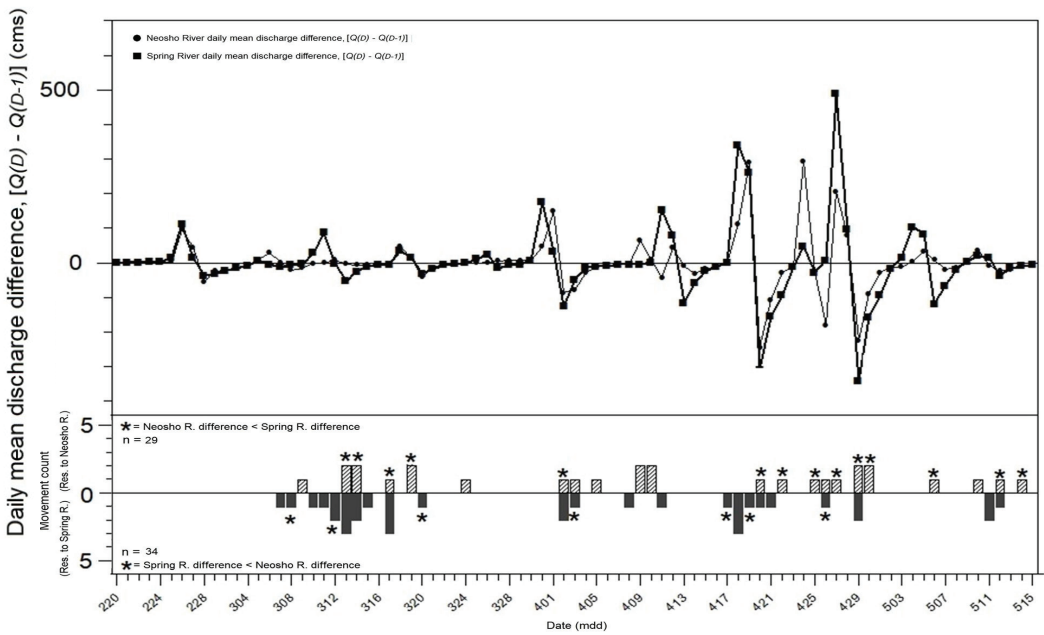

Figure 7. Number of choices of river (Neosho or Spring) in relation to change in change in discharge from the previous day, Feb 15-May 15, 2013. No fish moved into rivers from Feb 15 through Feb 19. Asterisk (*) indicates choice of river with the highest change in discharge.

Our tag detections for telemetered Grand Lake female paddlefish also indicated, however, that not all females made annual migrations into one or both rivers, suggesting that some female fish do not spawn in successive years, but have a two-year spawning periodicity. Four of 10 fish found in the NR or SR, or both, in 2013 were not detected in either river in 2012. Similar conclusions have been reached in a nearby paddlefish stock. Leone, Stoeckel, and Quinn (2012) reported levels of gravidity 48-73% across multiple years and sites, indicating some multi-year spawning intervals in Arkansas River fish in Arkansas. In contrast, both Scholten and Bettoli (2005) and Lein and DeVries (1998) reported annual spawning in southern stocks (Tennessee and Alabama, respectively). Even within a climatic zone typically associated with annual spawning, non-annual spawning in various species, including paddlefish, may be a result of several causes, including maturation timing problems, egg reabsorption, or energy limitations associated with productivity in a particular river system (Rideout, Rose, and Burton 2005). Delayed female spawning may also be a result of unfavorable environmental conditions (e.g., discharge and temperature) affecting the rate of gonadal recrudescence. The ability to accelerate or delay maturation may also be an adaptive life history trait, especially for females (Bell 1980; Quinn and Ross 1985). In addition, the minority non-annual spawners take longer to detect, and thus may be less likely to be identified than annual spawners in tagging studies.

One cause of reproductive delay that cannot be ruled out might be stress associated with the tagging process. The presence of an ultrasonic tag in the peritoneal cavity of a gravid female may result in increased egg retention, reduced fecundity, or otherwise aberrant reproductive physiology. Research with internally telemetered steelhead *Oncorhynchus mykiss*, for example, showed an increase of 47% in egg retention compared to control fish (Berejikian et al. 2007). The authors noted no significant behavioral changes between telemetered and control fish, however, so presumably migration and spawning behaviors were unaffected. In our study, there were no obvious indications that surgical implantation hindered or modified their pre-spawning behavior or spawning. In an earlier telemetry study on Grand Lake paddlefish, Johnston and Gordon (2010) noted that of 11 mature females implanted in December 2007, three were confirmed to migrate up the NR the following year. Another six implanted fish were located in the Twin Bridges staging area and potentially migrated up the SR.

River choice: Results on river choice in this study were restricted primarily to 2011 because of the dwindling numbers of fish able to be tracked after that year. Because of non-annual spawning in some female paddlefish, more results were available for 2013 than for 2012. Results from 2011, the year with the strongest data, showed no clear preference for choosing the SR over the NR during the month of April, even though discharge was anomalously much higher in the SR than in the NR that year. Data from other years are more difficult to interpret. In 2012, NR discharges tended to be higher, although base flows for both NR and SR were extremely low throughout the migration period except for two flood pulses, the latter of which occurred when fish were no longer migrating from the reservoir to the river. In 2013, SR discharges tended to be higher than in the NR throughout the migration season. These discharge patterns are far from the patterns most commonly observed and make it difficult to assess river choice as it would occur under more typical higher spring discharges in the NR. For example, the low discharges in spring 2013 and 2014 resulted in lingering behavior of paddlefish at the NR and SR mouths at Twin Bridges State Park; strong upriver movements were not observed in the few tagged fish at large. A larger number of tagged fish would have been useful for evaluating river choice during a high-discharge year when NR discharges far exceeded those of the SR; this situation did not occur in this study.

While our results do not imply any statistically verified preference for the NR, the slightly higher numerical use of the NR, although lower in discharge, than the SR in 2011 is not inconsistent with two recent studies on Grand Lake paddlefish indicating greater availability

of spawning habitat in the NR than the SR (Schooley and Neely 2018) and a much higher percentage of NR-origin paddlefish than SR-origin paddlefish among recruits to the Grand Lake stock fishery (Schooley, Whitledge, and Scarnecchia 2021). Schooley and Neely (2018) used sonar to compare spawning habitat availability between the two rivers and reported greater abundance of spawning habitat in the NR than the SR, a greater distance to the first spawning barrier (Chetopa), facilitating migration, along with a larger watershed. In a follow-up study, Schooley et al. (2021) used otolith microchemistry on harvested Grand Lake paddlefish and found that 87% of the harvested fish were NR origin versus 7% SR origin, with 6% undetermined, indicating the preferential success of the NR in producing Grand Lake paddlefish. Those two studies showing habitat quality and recruitment success in the NR, which were interpreted as supporting the NR as the preferred paddlefish spawning river, are not inconsistent with this study. It is not clear if the higher recruitment of fish from the Neosho River than the Spring River (Schooley, Whitledge, and Scarnecchia 2021) results from more spawning in that river or just more successful recruitment of fish from a given amount of spawning. In the latter case, fish attempting to spawn in the Spring River, with the river acting as a spawning sink, would be selected against in future generations.

Results of this study indicate that under observed discharge conditions of 2011-2014, both rivers provided important pre-spawning staging habitat and telemetered fish ascended both rivers each spring regardless of flow conditions in the rivers. Many paddlefish movements in spring, including individual choice of river ascended, were not necessarily dictated by, nor statistically associated with, patterns of NR and SR discharges or changes in discharges. The close proximity of the mouths of the two rivers (<1 km), the gentle gradients at the mouths of both rivers, and the short movements made may not result in a substantial energetic cost for using lower portions of both rivers as pre-spawning staging areas prior to their actual choice of a spawning river. In some years, including years of this study, regional and local weather events will also

result in similar patterns of river hydrology and temperature in the two rivers. This similarity was evident in water temperatures across rivers and synchronous hydrology for 2011 – 2013 (Schooley and Johnston 2015). Daily average river temperatures (January 1 to June 4, 2012) were closely correlated between the two rivers: (Pearson Correlation r = 0.99 p < 0.0001; Schooley and Johnston 2015). This strong synchronicity of the NR and SR in temperature and discharge does not occur every year but may have favored utilization of both rivers during years of our study. In other years, e.g., with exceptionally high NR discharge from high rainfall in the upper watershed and significant water releases from John Redmond Reservoir in Kansas, greater differences occur between NR and SR discharges and water temperatures.

In addition, other factors not investigated in this study may influence river choice, including water chemistry, specific temperature conditions, and other unrecognized factors. A much larger, more directed study with more fish and more diverse environmental monitoring would be needed to thoroughly investigate such possibilities.

Potential information on spawning, reproduction, and recruitment: Results of this study and other data from the Oklahoma Department of Wildlife Conservation Paddlefish Research Center (PRC) contribute indirect information on spawning occurrence, reproduction, and recruitment. Although some fish entered both rivers in all four years, in 2014, the low river discharge that year compared to 2011-2013 undoubtedly reduced availability of spawning habitat and substrates, In the low discharge year of 2014, only one harvested female was found spawned-out at the PRC, despite the PRC remaining open an additional two weeks until May 15. In contrast, numbers of spawned out fish in the other three study years as well as earlier years were more prevalent: 2008 – 92, 2009 – 123, 2010 – 31, 2011 – 40, 2012 – 53, and 2013 – 62. The timing of harvest of these spawned-out females in all years was synchronous with a declining Neosho River hydrograph after a cresting event in excess of 283 m³/sec (10,000 cfs; ODWC, unpublished data). Based on our study showing

prevalent annual spawning of females, or the capability of it, and the different interannual frequencies of spawned-out females in the angler harvest at the PRC, we conclude that successful spawning occurred in 2011-2013, but probably not in 2014.

Information on spawning activity and success over the years is scarce in many stocks. Few studies have been able to collect sufficient information on paddlefish to characterize reproductive success or recruitment as occurring every year, in most years, intermittently, or, in some cases even more sporadically (i.e. episodic; Scarnecchia et al. 2014). The suite of factors and conditions leading to successful reproduction, including river discharge, temperature, their duration and timing, and their effects on paddlefish spawning movements are recognized but not fully understood (Purkett 1961; Wallus 1986; Stancill, Jordan, and Paukert 2002). Previous analyses indicated that a benchmark of 283 m^3/sec elicits an upstream migratory response from Grand Lake paddlefish, but that sustained, elevated river stages are required to submerge and maintain gravel shoals used for egg deposition. In such a case, prolonged higher river discharge in spring may provide a longer window for upriver movement, resulting in longer distances traveled upstream, opening additional substrates and habitats for spawning, hatching, and survival of young.

The timing of high discharge and river temperatures may be hypothesized to play a role in recruitment success for paddlefish in Grand Lake. Early flow events (such as the fluctuating water levels of early March 2011) are not likely to be associated with sufficiently elevated temperatures to allow for egg hatching (>10°C; Wallus 1986). Both rivers flooded on June 2, 2013 and remained out of their respective banks for a duration of 4-5 days. Typically, the late timing of this event would not contribute to paddlefish spawning in the NR and SR (i.e. too late in the year), but the effects on recruitment are unknown. Therefore, flow events occurring mid-March to mid-April, when water temperatures are warmer, are more likely to provide ideal conditions for upstream movement and successful spawning

and hatching. Follow-up studies in years of different NR and SR discharges may provide more information on the roles of discharge, including timing, and temperature on river choice, spawning success, and recruitment.

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