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Recruitment contributions and natal fidelity in tributary rivers of the Grand Lake, Oklahoma, Paddlefish stock

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Abstract

Microchemistry of sectioned dentary (lower jaw) bones was used to determine natal river (Neosho, Spring or Elk River) of paddlefish *Polyodon spathula* (Walbaum) in the economically important snag fishery in Grand Lake, northeastern Oklahoma, and to assess the relative importance of the tributary rivers as sources of recruits to the fishery. Geological differences between the Neosho River and Spring River watersheds resulted in large differences in water strontium:calcium (Sr:Ca) ratios reflected in dentary Sr:Ca for paddlefish from each river. Dentary core Sr:Ca signatures were used to infer natal river for paddlefish harvested over the period 2008–2018. Most harvested fish (87%) were identified as Neosho River origin, and 7% were within the predicted range for Spring River origin (6% undetermined). Relative frequencies of Neosho River and Spring River-origin fish (the latter, all ≤10%) differed among cohorts but did not differ among years, locations or sexes. Results corroborate a sonar survey of spawning substrates that concluded that the Neosho River has higher potential value for paddlefish spawning and recruitment than the Spring River. No evidence of natal river fidelity was found. Results highlight the importance of maintaining habitat conditions and inform harvest management regulations required for paddlefish spawning, recruitment and sustainability.

KEYWORDS
conservation, fidelity, habitat, management, microchemistry, spawning

1 | INTRODUCTION

Spawning and reproduction leading to successful recruitment have long been identified as critical shortcomings in efforts to manage paddlefish *Polyodon spathula* (Walbaum) sustainably (Russell, 1986; Scarnecchia et al., 2019; Sparrowe, 1986). Losses of spawning habitat and natural river function have been implicated in reproduction and recruitment failure in paddlefish (Gerken & Paukert, 2009; Sparrowe, 1986). Hatchery production has partially mitigated for some of the habitat losses and reproductive failures (Schwinghamer et al., 2019; Shelton et al., 2019), and some 20th Century reservoirs have provided new rearing habitats (Scarnecchia et al., 2019). However, long-term survival of the paddlefish as a wild species depends on identifying and protecting spawning rivers (and river segments) and their habitats.

Few direct observations and evaluations of paddlefish spawning and habitat have been conducted (e.g. Crance, 1987; Purkett, 1961). Although sonar technology has enabled more specific descriptions of river substrates associated with potential spawning habitat (Schooley & Neely, 2018), most spawning habitat assessments have been indirect, identifying which specific habitats telemetered paddlefish occupy in spring. Subsequent egg and larval sampling has occurred at those locations to confirm spawning, but often with limited success (Firehammer et al., 2006; Miller et al., 2008, 2011; Tripp et al., 2019). Several studies have provided some evidence that both movements and probable spawning locations vary among reaches depending on the year (Firehammer et al., 2006; Rugg et al., 2019). In many cases, pre-spawning paddlefish, given a choice of rivers, chose to ascend the river with the higher discharge. Some interannual fidelity to specific rivers, river reaches and suspected spawning sites has also been detected (Braaten et al., 2009; Firehammer & Scarnecchia, 2007), despite not with the preciseness of some other North American freshwater species such as northern-like *Esox lucius* L. (Miller et al., 2001) or lake trout *Salvelinus namaycush* (Walbaum) (Binder et al., 2015).

More recently, improvements in calcified structure microchemistry, a technique used in fisheries for a half-century (Bagenal et al., 1973; Tómasson, 1978) but more recently refined and improved (Whitledge et al., 2019), have enabled biologists to ascertain natal river origin, sometimes identify river segment, and characterise movement patterns of individual fish (Abell et al., 2018; Laughlin et al., 2016; Pracheil et al., 2014; Rude & Whitledge, 2019). Concentrations of some chemical elements present in calcified structures (including paddlefish dentary bones) are strongly correlated with corresponding elemental concentrations in the waters in which a fish lives (Bock et al., 2017; Pracheil et al., 2014). Paddlefish dentary Sr:Ca ratio has been demonstrated to reflect sequential changes in water Sr:Ca to which fish were exposed (Bock et al., 2017). Dentary bone microchemistry has been successfully used to infer natal river for age-0 paddlefish sampled from the middle Mississippi River (Rude & Whitledge, 2019).

The Grand Lake – Neosho River – Spring River complex in northeastern Oklahoma (including the Elk River, a smaller discharge tributary; Figure 1) supports the state's largest and most economically important paddlefish stock and recreational fishery (Jager & Schooley, 2016; Melstrom & Shideler, 2017). Successful reproduction in the system is thought to be closely linked to environmental conditions, such as high river discharge of long duration, appropriate water temperature and spawning habitat availability (Schooley & Neely, 2018). Recruitment of strong year classes is episodic (Scarnecchia et al., 2011, 2013).

Oklahoma Department of Wildlife Conservation (ODWC) managers need to identify the comparative importance of the two major rivers (the Neosho River and Spring River) thought to support natural reproduction and recruitment. They can then protect critical spawning habitat better and ensure long-term population and fishery sustainability. The mouths of the two rivers enter Grand Lake immediately adjacent to each other (Figure 1). Although the Neosho River has traditionally been the main paddlefish fishing river (Ambler, 1994; Gordon, 2009; ODWC, 1986) and thought to be the primary spawning river, direct evidence of the two rivers' relative importance as sources of recruits to the Grand Lake stock and fishery has not been obtained. It is also unknown if the relative use of these two rivers for spawning is consistent among years or differs between the occasional strong cohorts and the more common moderate-to-weak cohorts. In addition, understanding of the degree of natal river fidelity by paddlefish would aid the evaluation of how critical a particular river's habitat is for spawning and early life history in this stock. In evolutionary terms, strong site fidelity would imply that one habitat is consistently preferable to others for reproductive success (Binder et al., 2015; Leggett, 1977), and thus deserving of the greatest habitat protection.

In this study, paddlefish dentary bone microchemistry was used to infer natal river and early life history of paddlefish in the Grand Lake watershed. In summer 2013, prior to the start of the study, water samples collected in summer indicated that geological differences between the Neosho and Spring River watersheds resulted in large differences in the water strontium:calcium (Sr:Ca) ratio between these two rivers. Thus, it was expected that measurements of Sr:Ca ratio in the centre of the dentary bone (i.e. the portion of the bone that reflects the fish's early life history) and matched to Sr:Ca signatures of paddlefish spawning tributaries would allow

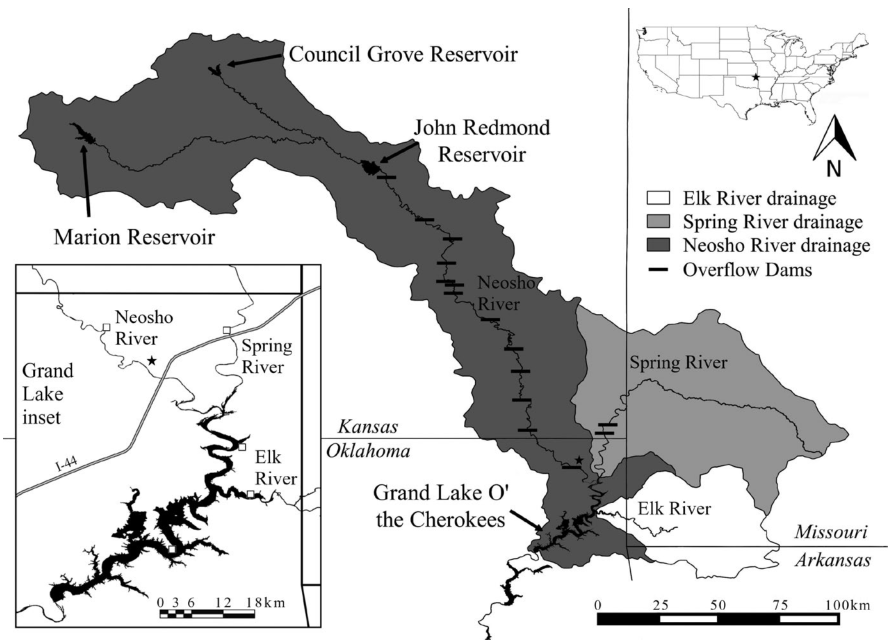

FIGURE 1 Map of Grand Lake watershed in southeast Kansas, southwest Missouri and northeast Oklahoma (modified from Schooley & Neely, 2018) depicting locations of water sample collection sites (squares, see Whitledge & Schooley, 2020). Miami, Oklahoma, is depicted by a star

identification of natal river for paddlefish harvested from the Grand Lake watershed.

The objectives of this study were to (1) estimate the relative contributions of the Neosho and Spring rivers as natal environments for paddlefish in the Grand Lake watershed stock and fishery; (2) determine whether relative importance of the Neosho and Spring rivers as paddlefish recruitment sources differed among strong, intermediate and weak cohorts; (3) assess the relative frequency of natal river fidelity for adult fish caught in the Neosho and Spring rivers; and (4) integrate results with habitat knowledge to inform decisions for the long-term management of the fishery.

1.1 | Study area

The study was conducted on the paddlefish stock inhabiting the Grand Lake O' the Cherokees (Grand Lake) watershed (Figure 1). Grand Lake, completed in 1940 as a Works Progress Administration (WPA) project, is an 18,817-ha impoundment behind Pensacola Dam on the Grand River (so-named extension of the Neosho River) in northeastern Oklahoma. The project was constructed mainly for flood control and hydropower generation. Grand Lake is fed by two major tributaries, the Neosho and Spring rivers, which drain distinct ecoregions and likely serve as the primary spawning areas for the Grand Lake paddlefish stock. A third tributary, the Elk River, likely plays a lesser role in paddlefish recruitment, as no spawning has been observed, but paddlefish are regularly encountered there. The naturally recruiting paddlefish stock of Grand Lake has high genetic importance to the greater Arkansas River stock (Schwemm et al., 2015).

The primary headwater tributary of Grand Lake is the Neosho River, which lies within the Osage Plains physiographical region typified by prairies with thick, productive soils and soft shales with interbedded sandstone and limestone (Adamski et al., 1995). The Neosho River basin (17,423 km^2, Figure 1) includes two large dams that impound water on the Neosho River in Kansas creating Council Grove Lake and John Redmond Reservoir, and 12 low-head (overflow) dams between John Redmond Dam and the Oklahoma border, the lowermost at Chetopa, Kansas (Neely et al., 2014, 2015; Scarnecchia et al., 2013). There is an additional overflow dam at Miami Park in Miami, Oklahoma. Active pre-spawning paddlefish staging and snagging sites exist at Miami Park and, sufficiently high flows permitting, at Chetopa (Bonislawsky, 1977; Neely et al., 2015).

From its origin in Southwest Missouri, the Spring River flows within the Springfield (Ozark) Plateau physiographical region typified by deciduous forests with weathered, acidic soils and chert limestones (Adamski et al., 1995), and drains 6708 km^2. Land use in the Spring River basin is transitory, although primarily agricultural (52%–85%), and includes regions of forested (15%–45%) and mined lands (3%). Schooley and Neely (2018) further described the substrates and hydrology of the Neosho and Spring rivers.

Both the Neosho and Spring rivers have been impacted by heavy metal contamination as a result of the extensive zinc–lead mining undertaken on lands draining both watersheds in the late 19th and early 20th centuries (Gibson, 1972; Manders & Aber, 2014; Weidman, 1932). As of 2020, concerns persist over the effects of heavy metal contamination on the aquatic and terrestrial life of the area (Angelo et al., 2007; Beattie et al., 2017; EPA, 2019; Kiner et al., 2005), including paddlefish reproductive development (Schooley et al., 2020).

The third and lesser tributary river of Grand Lake is the 56.6 km Elk River, which originates in southwest Missouri (Figure 1). The basin drains 2675 km^2, including portions of Northwest Arkansas, and, like the Spring River, is confined within the Ozark Plateau physiographical region. Statistics and bathymetric data for all three rivers within Oklahoma and Missouri were provided by Hunter et al. (2017).

These three tributary rivers and their intermixed waters in the upstream half of Grand Lake comprise the study area for this project, as these encompass the pre-spawning staging areas and spawning habitats for paddlefish (Figure 1).

2 | MATERIALS AND METHODS

2.1 | Water chemistry

Application of calcified structure microchemistry for inferring fish environmental history requires confirmation of spatial differences in water chemistry within the study area. Water samples were collected during spring 2018 and 2019 to verify persistence of differences in water Sr:Ca for the Neosho and Spring rivers that were observed in 2013 and to assess spatial variability in water Sr:Ca and Ba:Ca in Grand Lake and its principal tributaries (Neosho, Spring and Elk rivers), specifically during the paddlefish spawning season. Forty-five water samples were collected in spring 2018 and 2019 (approximating a low-water year and high-water year, respectively; Schooley & Neely, 2018) from five sites selected to represent each of three tributary rivers (Elk, Neosho and Spring), the Grand River approximately 11 km downstream the confluence of the Neosho and Spring rivers, and Grand Lake approximately 18 km below the confluence of the Elk and Grand rivers (Whitledge & Schooley, 2020; Figure 1).

Water samples were analysed for strontium, barium and calcium concentrations. Water samples were filtered using acid-cleaned polypropylene syringes and Whatman Puradisc (GE Healthcare Life Sciences, Pittsburgh, PA, USA) 0.45-µm polypropylene syringe filters (Shiller, 2003) and stored in acid-cleaned polypropylene bottles prior to shipment for analysis at the Center for Trace Analysis, University of Southern Mississippi. Samples were analysed for ^{44}Ca, ^{88}Sr and ^{137}Ba using a Thermo-Finnigan Element 2 (Thermo Fisher Scientific, Waltham, MA, USA) inductively coupled plasma mass spectrometer (ICPMS) (Shiller, 2003). Precision of analyses based on repeated measurements of standards was better than ±2% (2 SD). Elemental concentration data from water samples were converted to Sr:Ca and Ba:Ca ratios (mmol/mol). However, Ba:Ca was not found to be useful for distinguishing Neosho River-origin from Spring River-origin paddlefish (Whitledge & Schooley, 2020). Therefore, only water and dentary bone Sr:Ca data are reported here. Differences in mean water Sr:Ca among collection sites were assessed using a generalised linear mixed model followed by Tukey's HSD test for multiple comparisons.

2.2 | Dentary chemistry

Dentary bones for analysis of Sr:Ca were obtained from samples archived by ODWC from paddlefish harvested from Grand Lake and the Neosho River over the periods 2008–2009, 2014–2016 and 2018. Only 2 years of dentaries were available for Spring River (2008–2009) because the fishery for paddlefish was closed in 2010 (Schooley et al., 2014). Age and cohort were previously assigned for harvested individuals at the University of Idaho as described in Scarnecchia et al. (2011). From a total collection of 32,451 fish for which age were estimated, samples of sectioned dentary bones representing approximately 25 fish per harvest location, per harvest year, and each of three cohorts from strong (1999; $n = 355$), intermediate (2008; $n = 200$) and weak (2004; $n = 200$) recruitment years were selected for analysis. As the annual harvest primarily consists of sexually mature paddlefish, maturation rate (5 years for males and 8 years for females) rendered mature cohorts (within sex) abundant only in certain harvest years post-maturity. The 1999 cohort dominated harvest in 2008–2018; therefore, this cohort was examined for all locations and each selected year. In all, 755 dentary samples were selected for analysis.

Within a priori-selected harvest year/cohort/harvest location groupings, selection of dentaries consisted of a three-step, weighted, randomised process. First, fish harvested during the peak season (calendar day 75–110) were identified and given a value of 1 (aka "peak" integer), otherwise 0. Second, fish with "spawn" in the comments (noting that the fish had already spawned or was in the process of expressing eggs) were identified and given a value of 1 (aka "spawn" integer), otherwise 0. A fish harvested during the peak season and/or having spawned or ready to spawn was presumed a higher likelihood of the harvest location accurately representing the spawning river. For example, a spawned-out female paddlefish harvested in the Neosho River in early April had a high likelihood of having deposited her eggs in the Neosho River (versus the Spring River). Third, all fish were assigned a random integer that was added to peak and spawn integers to serve as a selection value. The selection values were numerically sorted, and the largest 25 were selected. The next five largest were identified as alternates when available. Fish of hatchery origin, as notated by the presence of a coded wire tag, were not eligible for selection.

The weighting process biased selection towards females due to the spawn integer, but this was anticipated. Restricting the sample selection to one sex or to a balanced sex ratio was not possible given the fish available and the lack of spawning observations in some harvest years. Male paddlefish are capable of spawning on multiple occasions or at multiple locations within a single season; thus, it was deemed acceptable that the selection process weighting biased the results to females. Actual sex ratios of selected dentary samples used in this study are shown in Table 1.

Dentary bone samples were analysed for strontium and calcium concentrations using a Thermo X-Series2 inductively coupled plasma mass spectrometer (ICPMS) coupled with a CETAC Technologies LSX-266 laser ablation system. The laser was used to ablate a line transect (beam diameter = 25 μm, scan rate = 5 μm/s, laser pulse rate = 20 Hz, laser energy level = 35%) across the core of the sectioned dentary bone (within the first annulus, passing through the centre of symmetry). Each sample analysis was preceded and followed by 30 s argon gas blank measurements. Two reference standards (MACS-3 and NIST-1486) were analysed in triplicate every 12–15 samples to enable quantification and correction of possible instrumental drift (Pracheil et al., 2014). Isotopes assayed included ^{43}Ca and ^{86}Sr. Correction for gas blank and drift effects and conversion of raw isotopic counts to elemental concentrations (μg/g) were performed using a Microsoft Excel macro (GeoPro) developed by CETAC Technologies. Elemental concentration data were then used to calculate molar Sr:Ca ratios (μmol/mol) along the laser ablation transect for each sample.

2.3 | Assignment of natal river: overall and by cohort

Assignment of natal river for each paddlefish required characterisation of dentary Sr:Ca ratios that were representative of fish from each potential natal river (Neosho River, Spring River, or Elk River). Age-0 paddlefish collected from their natal river could theoretically have been used to characterise dentary Sr:Ca signatures for each of the Grand Lake tributaries, but were not available (no sampling programmes target age-0 paddlefish in the study area). Thus, it was not possible to characterise location-specific chemical signatures from direct measurements of dentary bone microchemistry on fish of known environmental history. Instead, ranges of dentary bone Sr:Ca characteristic of the Neosho, Spring and Elk rivers were estimated from water chemistry data (from spring 2018 and 2019 sampling and prior collections) and a linear regression relating water and dentary bone Sr:Ca (Bock et al., 2017). Minimum and maximum water Sr:Ca values for each river were entered into the regression equation to predict upper and lower limits of dentary bone Sr:Ca for Neosho River-origin, Spring River-origin and potential Elk River-origin fish. Maximum estimated dentary bone Sr:Ca for each river was defined by the upper 95% confidence limit of predicted dentary Sr:Ca at the maximum observed water Sr:Ca value for each river; likewise, minimum estimated dentary bone Sr:Ca for each river was defined by the lower 95% confidence limit of predicted dentary Sr:Ca at the minimum observed water Sr:Ca value for each river (Laughlin et al., 2016). The predicted range of dentary Sr:Ca for Neosho River-origin paddlefish was 474–729 μmol/mol, whereas the predicted range of dentary Sr:Ca for Spring River-origin paddlefish was 36–338 μmol/mol. Predicted range of dentary Sr:Ca for Elk River-origin paddlefish was

TABLE 1 Numbers of paddlefish identified by river origin (Neosho, Spring or not definitive) using dentary core Sr:Ca

	Paddlefish	Origin		
		Neosho (%)	Spring (%)	Not definitive
(a) Cohort				
1999	355	308 (87)	16 (5)	31
2004	200	179 (90)	16 (8)	5
2008	200	169 (85)	20 (10)	11
Totals	755	656 (87)	52 (7)	47
(b) Collection year				
2008	75	56 (75)	6 (8)	13
2009	79	64 (81)	2 (3)	13
2014	150	128 (85)	12 (8)	10
2015	149	136 (91)	10 (7)	3
2016	152	140 (92)	8 (5)	4
2018	150	132 (88)	14 (9)	4
Totals	755	656 (87)	52 (7)	47
(c) Harvest location				
Grand Lake	354	305 (86)	29 (8)	20
Neosho River	348	312 (90)	21 (6)	15
Spring River	53	39 (74)	2 (4)	12
Totals	755	656 (87)	52 (7)	47
(d) Sex				
Female	320	281 (88)	22 (7)	17
Male	435	375 (86)	30 (7)	30
Totals	755	656 (87)	52 (7)	47

Note: Study data are arranged for comparison by (a) cohort, (b) collection year, (c) harvest location and (d) sex. The percentage of Neosho and Spring River origin is also shown in parentheses.

10–306 µmol/mol. Dentary bone core Sr:Ca data (mean of 10 values from a 25 µm segment of the laser ablation transect, centred on the dentary bone primordium) for each harvested fish were compared with predicted ranges of dentary Sr:Ca values representative of the Neosho, Spring and Elk rivers to assign natal river to each individual. Fish with dentary core Sr:Ca ≤ 306 µmol/mol were classified as Elk River or Spring River-origin fish, fish with dentary core Sr:Ca between 307 and 338 µmol/mol were identified as Spring River-origin fish, and individuals with dentary core Sr:Ca between 474 and 729 µmol/mol were classified as Neosho River-origin fish. Natal river could not be identified for paddlefish that had dentary core Sr:Ca between 339 and 473 µmol/mol; these fish were assigned to an "unknown origin" category. A chi-square test was used to assess whether the relative frequency of individuals that originated in each river differed between strong and weak cohorts or between cohorts produced prior to versus after the Spring River fishery closure in 2009.

2.4 | Natal river fidelity

Data to address natal origin fidelity were obtained from the same set of dentary bone samples. Fidelity of adult paddlefish harvested from the Neosho and Spring rivers to their natal river was assessed by comparing natal river assigned from dentary core Sr:Ca with their known harvest location. Relative frequency of individuals exhibiting natal river fidelity was calculated for the sample of fish from each river. A Chi-square test was used to assess differences in relative frequency of individuals exhibiting natal site fidelity between the two rivers. In all tests, $p < 0.05$ was required for significance.

3 | RESULTS

3.1 | Water chemistry

Data from 2013, 2018 and 2019 water samples revealed a large difference in water Sr:Ca ratio between the Neosho and Spring Rivers (Figure 2) that resulted in non-overlapping ranges of predicted dentary bone Sr:Ca for Neosho- and Spring River-origin paddlefish. Grand Lake and Grand River had intermediate water Sr:Ca compared with the Neosho and Spring rivers, reflecting the mixture of Neosho River and Spring River water downstream of the confluence of these two rivers. Both Neosho and Spring River water Sr:Ca ratio also differed from Grand Lake. The Elk River water Sr:Ca ratio was lower than all other sampling locations.

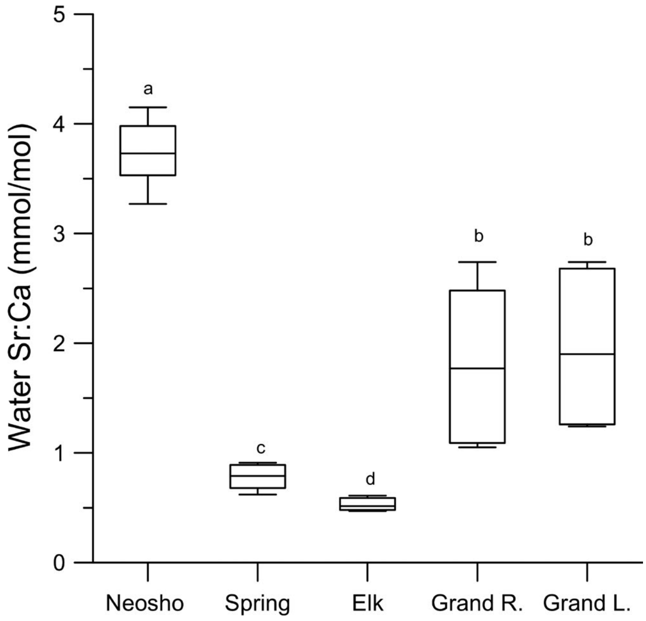

FIGURE 2 Boxplot showing median, interquartile range and range of water Sr:Ca for samples collected from the Neosho River, Spring River, Elk River, Grand River (upper section of Grand Lake) and Grand Lake (at Shangri-La Marina) during spring 2018 and 2019 and from the Neosho and Spring rivers during June 2013. Sites denoted by different letters above boxplots have statistically different mean water Sr:Ca (generalised linear mixed model followed by Tukey's HSD test for multiple comparisons, $p < 0.05$)

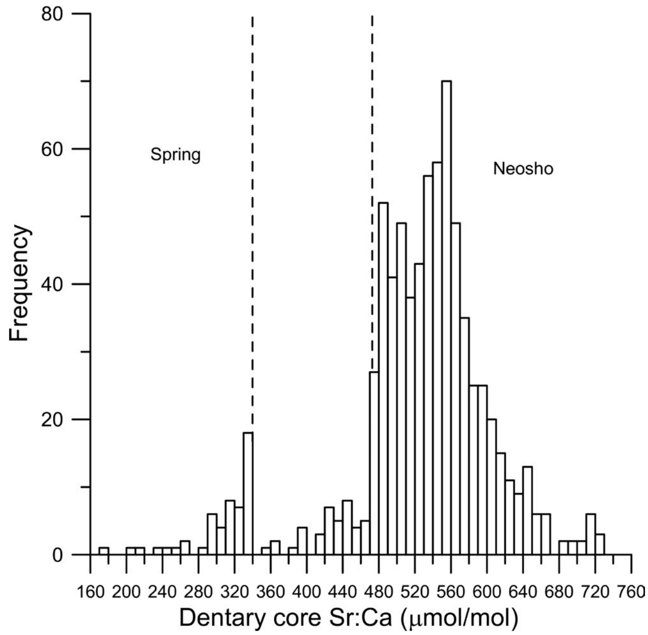

FIGURE 3 Frequency distribution of dentary bone core Sr:Ca for Paddlefish ($n = 755$) harvested from the Grand Lake stock during 2008, 2009, 2014, 2015, 2016 and 2018. Vertical dashed lines indicate the upper limit of predicted dentary bone Sr:Ca for Spring River-origin fish (338 μmol/mol) and the lower limit of predicted dentary bone Sr:Ca for Neosho River-origin fish (474 μmol/mol)

3.2 | Dentary chemistry: natal river assignment

Of the 755 paddlefish analysed, 87% had dentary core Sr:Ca ratios within the predicted range for Neosho River origin and 7% had dentary core ratios within the predicted range for Spring River (Table 1; Figure 3). Relative frequencies of paddlefish with dentary core ratios within predicted ranges for the Neosho and Spring rivers were marginally different among cohorts, $\chi^2(2, 708) = 5.88$, $p = 0.053$, although fish with dentary core ratios within the predicted range for Spring River-origin fish represented ≤10% of individuals in each of the three cohorts sampled (Table 1a). Relative frequency of fish with Sr:Ca dentary core ratios within the predicted range for the Spring River was higher among individuals sampled from the 2008 cohort than the 1999 cohort, $\chi^2(1, 513) = 5.83$, $p = 0.015$, but proportions of Neosho River-origin fish and fish with dentary core ratios within the predicted range for the Spring River did not differ between the 1999 and 2004 cohorts, $\chi^2(1, 519) = 2.24$, $p = 0.13$, or between the 2004 and 2008 cohorts $\chi^2(1, 384) = 0.64$, $p = 0.42$. Relative frequencies of Neosho River-origin paddlefish and fish with dentary core ratios within the predicted range for Spring River-origin fish did not differ among collection years (Table 1b; $\chi^2(5, 708) = 4.56$, $p = 0.47$, collection locations (Table 1c; $\chi^2(2, 708) = 1.77$, $p = 0.41$, or between males and females (Table 1d; $\chi^2(1, 708) = 0.0055$, $p = 0.94$. Fifty-two paddlefish had dentary core Sr:Ca ratios within the predicted range for Spring River-origin fish (Table 1). Eighteen of these individuals had dentary core ratios ≤ 306 μmol/mol, the upper predicted limit of dentary core ratios for an Elk River-resident fish.

Forty-seven fish had dentary core Sr:Ca ratios between the predicted upper limit of dentary ratios of Spring River-origin fish (338 μmol/mol) and the predicted lower limit of dentary core ratios for Neosho River-origin fish (474 μmol/mol); thus, their natal river could not be identified (Table 1; Figure 3).

3.3 | Dentary chemistry: natal river fidelity

Spring River-origin fish that were harvested from the Neosho River were identified in 5 of the 6 collection years (all except 2009) and Neosho River-origin fish harvested from the Spring River in the two years prior to the 2010 fishery closure. However, no effect of harvest location on the relative frequency of Neosho River-origin and Spring River-origin paddlefish was found in the samples (Table 1c; $\chi^2(2, 708) = 1.77$, $p = 0.41$.

4 | DISCUSSION

4.1 | Habitat selection and implications for management

The predominant usage of the Neosho River by Grand Lake stock paddlefish is consistent with typical paddlefish spawning habitat documented in other studies. Range-wide, paddlefish spawning rivers during the spawning season have often been characterised as flood-prone, turbid (Russell, 1986) and debris-laden.

This characterisation describes the current Neosho River in its lower reaches in Oklahoma and south-eastern Kansas, despite the upriver impoundments. Lower river, low-head, overflow dams (e.g. at Miami [Oklahoma], Chetopa [Kansas] and 11 more upriver) impound little water and trap little sediment compared with the impoundments. There are also few natural lakes or wetlands in the watershed; most of the runoff is derived from the 102 cm average annual rainfall in the basin (Branson, 1967). Many characteristics of a natural flow regime (Poff et al., 1997) persist in the lower Neosho River used by spawning paddlefish.

Other major paddlefish spawning rivers share most of these features of spawning habitat. One of these rivers, at least historically, was the Marais de Cygnes (Kansas) and Osage River (Missouri), one of the most historically productive paddlefish river systems prior to impoundment. Like the Neosho, the upper Osage River is not primarily spring-fed by its tributaries (Payton and Payton, 2012) but historically functioned as more of a direct runoff system fed by rainfall. Purkett (1961) described the Osage River at the time he observed paddlefish spawning as rapidly flowing with a turbidity of 180 ppm. Flooding was common in pre-settlement times but is much more limited nowadays (Heimann et al., 2007). In the lower Yellowstone River of eastern Montana and western North Dakota, another important remaining paddlefish spawning river, spawning has not been observed, but egg and larval collections associate spawning with high discharge (often flood conditions, from both snowmelt and spring rains) and turbid, debris-laden waters typical of a rapid rise in discharge (Scarnecchia et al., 2019). Rapid rises in discharge have also been associated with spawning in other localities (Cumberland and Tennessee rivers: Wallus, 1986; Tombigbee River: O'Keefe et al., 2007).

As with many paddlefish rivers nationwide, the Neosho River has a long history of highly variable discharges and flooding. The river flooded 57 times in the 34 years prior to 1964 in southeastern Kansas, prompting public requests of the U. S. Army Corps of Engineers for flood control (Studley, 1996). The response was the construction of three flood control dams in the upper basin, with the lowermost, John Redmond Dam, completed in 1964. The dam system has provided flood control benefits, resulting in a stabilisation of flows (lower peaks during high discharges and higher flows during low discharges; Juracek, 1999; Studley, 1996). It fluctuates widely in discharge in response to rains and has continued to flood periodically after John Redmond was in place, resulting in spawning and recruitment benefits to paddlefish (Scarnecchia et al., 2013), but creating substantial local economic hardship (e.g. 1986: Miami, Oklahoma, Kiwanis Club, Undated; 2019: Mervosh, 2019). The meandering, low gradient (<0.38 m/km; Hunter et al., 2017), lower Neosho River also can back up behind a full Grand Lake, filling and overflowing the floodplain, exacerbating flooding in the City of Miami and downriver to Twin Bridges State Park, and necessitating the need to manage Grand Lake water levels to reduce impacts.

Impacts of river regulation on Neosho River function, however, have been greater near the dams than downriver. Discharge changes below John Redmond Dam were more substantial at sites near the dam (e.g. Burlington, Kansas, 8.5 km below the dam) but decreased greatly at downriver sites (e.g. Parsons, Kansas, 224.6 km below the dam), a difference attributed to the position of the dams high in the drainage basin, resulting in a much larger part of the drainage being unregulated as the distance from the dam increases (Studley, 1996). An even less substantial flood control benefit exists farther downriver at Chetopa and in Oklahoma, the area where the Grand Lake paddlefish inhabit. Juracek (1999) concluded that the dam alteration of flow regime and downriver sediment loads has not caused major or widespread alterations below the dam on channel degradation, channel morphology and downriver stability. Several factors influenced this result, including a bedrock and gravel stream bed, channel banks mostly of cohesive silt and clay, and a wide channel from previous floods, and mature tree cover in much of the riparian zone (Juracek, 1999).

The differential usage of the Neosho River compared with the Spring River cannot be explained, however, by a lack of rising discharge in the Spring River. Discharge during spawning season and paddlefish movements in the Spring River can be rapid and are also primarily driven by spring rains (Scarnecchia et al., 2013). Schooley and Neely (2018) concluded that differences in spawning habitat availability and suitable conditions associated with the spring rises provides another explanation. Their investigations using sonar to map spawning habitat availability in the two rivers, disclosed that although potential spawning habitat, measured as gravel substrate, was abundant in both rivers (69% of the Neosho River, 58% of the Spring River), the proportion of spawning habitat available for spawning in the Neosho River was much higher for a given discharge. River rises in spring led to higher proportional spawning habitat availability and the hydrograph patterns led to the inundated spawning habitat being available for a much longer period of time in spring. The difference relates in part to the longer length (745 km Neosho versus 209 km Spring) and larger watershed (17,423 km^2 Neosho versus 6708 km^2 Spring) of the Neosho River; river rises and falls in the Neosho River are typically more protracted. The Neosho River consistently provided longer sustained periods of elevated river stage and therefore longer periods for paddlefish to complete four phases critical to successful spawning and reproduction, including movement from staging areas to spawning habitat, spawning, incubation and hatch, and downstream dispersal of larvae (Schooley & Neely, 2018).

Although it was expected that paddlefish use the impounded waters of the lower Elk River during early life stages, it was possible that a small fraction of the fish with dentary core Sr:Ca ratios ≤306 μmol/mol may have originated in the Elk River. However, any contribution from the Elk River to the 1999, 2004, and 2008 cohorts in the Grand Lake watershed paddlefish stock was minimal (≤2% of the total number of fish sampled). This conclusion is supported by low, but consistent, usage of the Elk River by paddlefish year-round and a low incidence of snagging activity in the Elk River (potentially indicative of low fish abundance). Furthermore, spring staging areas for pre-spawning paddlefish were primarily observed upstream of the Elk River confluence (Figure 1), which may also discourage its usage by Grand Lake paddlefish.

4.2 | Overlapping signatures

There are at least three potential explanations for the occurrence of individuals with intermediate dentary core Sr:Ca ratios (i.e. between 339 and 473 μmol/mol) not clearly indicative of either the Neosho River or the Spring River. First, these fish may have exited their natal river into Grand Lake too soon after hatching to accrue a signature detectable with the LA-ICPMS technique. Paddlefish drift downstream as larvae (Jennings & Zigler, 2009) and, a bit later, move downstream volitionally. They could easily find themselves in Grand Lake, and its intermediate Sr:Ca signature, early in their first year of life. Second, the laser ablation transect may have narrowly missed the exact location within the first annulus of the dentary bone where the earliest structural growth was present, especially if the fish exited a river early in the first year. Third, the dentary bone, which is metabolically active and potentially subject to reabsorption and remodelling (Whitledge, 2017), may not have retained its natal river Sr:Ca ratio signature. This possibility seems less likely; there was no evidence of a central lumen (i.e. gap) in any of the sectioned dentary bone samples used in this study, a common characteristic of fin rays or fin spines of other species in which bone grown during early life was reabsorbed (Whitledge, 2017). These unassignable fish created only minor problems with interpretation due to their relatively low frequency among the samples. The higher relative contribution of Spring River fish in the 2008 cohort may be an artefact of a higher frequency of unassignable fish in 1999 (Table 1a) rather than an ecologically significant difference in river contribution to a cohort. Regardless of the mechanisms responsible and the creation of this minor interpretation issue, the unassignable individuals represented only 7% of all fish analysed. Their presence did not alter the primary finding that most paddlefish (87%) were of Neosho River origin across all three of the cohorts examined.

4.3 | River fidelity

Dentary bone core Sr:Ca ratio data coupled with harvest location information for individual fish indicated that harvested paddlefish did not exhibit strong natal river fidelity during presumptive upriver spawning migrations. This result was supported by a telemetry study of Grand Lake paddlefish (Schooley & Johnston, 2014) that found sometimes repeated exploration of both rivers by individual gravid female paddlefish during their pre-spawning movements in spring. These movements suggested opportunistic tributary river usage, where fish entered and spent time in multiple rivers within a season and across years, versus strict fidelity to one river (Schooley & Johnston, 2014). Although some spawning site fidelity cannot be ruled out and is strongly suggested in other paddlefish stocks (Braaten et al., 2009; Firehammer & Scarnecchia, 2007), the extremely close proximity of the mouth of the Neosho River and Spring River to each other and the easy access to each river by migratory fish would make it likely that fish would move freely between the rivers in response to flows, other cues or even disturbances such as boat traffic. Repeated entry into one river in spring would not necessarily rule out eventual fidelity to a natal river. More investigations are needed to answer this question.

4.4 | Management implications

The results, along with results on gravel spawning habitat availability from Schooley and Neely (2018), underscore the importance of habitat management, including maintaining river function and its variable flow regime, for paddlefish (Poff et al., 1997; Wohl & Merritts, 2007) in both rivers, but especially the Neosho River. Spawning conditions such as flood peaks must be maintained while minimising negative impacts to human inhabitants along the river.

The minor role of natal river fidelity found in this study also has harvest implications. In most years, pre-spawning Grand Lake stock paddlefish stage by February and early March in the upper end of Grand Lake. Harvest in Grand Lake increases in March but decreases in April as rises in discharge from spring rains draw nearly all pre-spawning fish into either the Neosho River or Spring River (Scarnecchia et al., 2013). Harvest patterns and tag recoveries indicated that, overall, paddlefish commonly use both rivers and move freely between them (Scarnecchia et al., 2013; Schooley & Johnston, 2014). If the results had indicated strong natal site fidelity, harvest would need to be managed carefully in each tributary. Recruitment and stock recovery potential would need to be more tributary-dependent. For the Spring River, closed to snagging since 2010, there remains a need to determine whether its *de facto* designation as a sanctuary has been effective in aiding natural recruitment to the Grand Lake paddlefish stock. At the time of the closure, it was assumed that the two rivers were used more equitably for spawning.

For the Neosho River, this study underscores the importance of balancing harvest opportunities with concurrent spawning requirements of paddlefish in this preferred river. The Neosho River is the predominant spawning river as well as the most productive and accessible river for snagging. Likely, Neosho River spawning areas are generally known (Schooley & Neely, 2018; Schooley & O'Donnell, 2016) to occur upstream of Miami Park, whereas boat-assisted and land-based snaggers target downstream areas between upper Grand Lake and Miami Park. As of 2021, the fishery in the Neosho River is open seven days per week, year-round, and both pressure and harvest peak during the prime spawning period of March and April. The fishery has become more mobile in the past decade as boats with advanced sonar equipment can more actively seek out fish, rather than snag anglers waiting at well-known fishing locations such as Connors Bridge and Miami Park for fish to arrive (Jager & Schooley, 2016). It is not specifically known if this higher-tech fishery provides additional disturbance to paddlefish staging and spawning, although the more dispersed, yet directed nature of the fishery (and the pursuit of large female fish) makes it likely. In this situation, consistent monitoring of recruitment takes on added importance.

Possibilities for reducing harvest or spawning disruption relevant to Grand Lake paddlefish, if necessary, are thoroughly reviewed and discussed by Schooley et al., (2014). Options to provide additional sanctuary for the Neosho River spawners, if deemed necessary, would include closure of specified locations of the river deemed critical habitat for spawning or staging (Schooley et al., 2014; e.g. Yellowstone-Sakakawea stock, North Dakota: Scarnecchia et al., 2019). Future changes may warrant protections of critical paddlefish habitat in the Neosho River, including further expansion of the snag fishery in space and time, and the expansion of harvest power through advances in fishing technology in pursuit of trophy individuals.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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