

FACTORS ASSOCIATED WITH PADDLEFISH
RESTORATION SUCCESS IN OKLAHOMA
RESERVOIRS: AVAILABILITY OF POTENTIALLY
SUITABLE SPAWNING SUBSTRATE IN RESERVOIR
TRIBUTARIES

By

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CHAPTER I

IDENTIFYING POTENTIALLY SUITABLE SPAWNING SUBSTRATE FOR AMERICAN PADDLEFISH USING AERIAL AND SIDE-SCAN SONAR IMAGERY

ABSTRACT

American Paddlefish (*Polyodon spathula*) were once widely distributed, but have been extirpated from parts of their native range, primarily due to habitat fragmentation and degradation brought on by dams. To mitigate losses in Oklahoma, restoration stocking has occurred in some reservoirs with variable success. One factor thought to contribute to successful restoration efforts is the availability of suitable hard substrates in reservoir tributaries used by Paddlefish for the attachment and incubation of their eggs. Using side-scan sonar and supervised classification of aerial imagery we classified 4,550 ha of river substrates upstream of the river-reservoir interface in 10 reservoir tributaries. Additionally, substrate composition and accuracy of substrate maps varied among rivers and was usually associated with river morphology. We found that in general substrate availability coincided with a reservoir's Paddlefish population status. Future research should focus on additional areas identified for substrate mapping as well as studies assessing the location of successful spawning efforts in systems with natural reproduction to further our understanding of suitable habitats.

INTRODUCTION

Fishes of the order Acipenseriformes are one of the oldest and most threatened groups of species, primarily because of anthropogenic factors leading to their declines (Unkenholz 1986; Jennings and Zigler 2000; Haxton and Cano 2016; Jaric et al. 2017). The range of Paddlefish *Polyodon spathula*, for example, has diminished from that of their historical distribution, including extirpation from four states in the US and Canada (Jennings and Zigler 2000). While there are a variety of factors cited for this decline, one of the most common is the impoundment of large rivers (Unkenholz 1986; Jennings and Zigler 2000). Reservoirs create a multitude of ecological challenges for native riverine fishes, such as habitat fragmentation and degradation as well as changes in thermal and flow regimes (Unkenholz 1986; McCartney et al. 2001; Graf 2005; 2006; Liermann et al. 2012). In the case of Paddlefish, one of the most deleterious is the blocking of access to, or inundation and sedimentation of, historic spawning grounds (Unkenholz 1986). Without adequate spawning substrate, reproductive efforts may be hampered or unsuccessful, resulting in the population declines and local extirpations that have been observed.

Like other Acipenseriformes, Paddlefish exhibit potamodromy as a life history strategy, making long migrations upstream in rivers to reach spawning areas (Bemis and Kynard 1997). Paddlefish complete their spawning migration in medium to large inland rivers after peak discharges in the spring (Unkenholz 1986; Graham 1997; Jennings and Zigler 2000), spawning then proceeds over hard substrates such as gravel and cobble with fertilized eggs adhering to these surfaces for embryonic development (Purkett 1961; Crance 1987; Jennings and Zigler 2000; Firehammer et al. 2006).

For Paddlefish populations that have adapted to impoundment conditions, the composition of substrates in associated tributaries is particularly important for Paddlefish persistence and reproductive potential (Jennings and Zigler, 2000; Firehammer et al. 2006). Without adequate spawning substrate in reservoir tributaries, Paddlefish reproductive success may be impaired (Unkenholz 1986; Jennings and Zigler 2000). For instance, Paddlefish

reintroduced into Lake Texoma, Oklahoma-Texas were able to survive, albeit at a low rate, and grow, but were not able to persist without additional stocking (Patterson 2009), suggesting that something was lacking related to spawning or larval survival. Elsewhere, various reservoirs like Lake Francis Case in South Dakota and Table Rock Lake in Missouri use supplemental stocking because of low or absence of Paddlefish recruitment to provide sustainable fisheries (Pierce et al. 2009; Hupfield et al. 2017). In Oklahoma, Paddlefish have been stocked in several large reservoirs with varying levels of success, and plans for additional stockings are being considered. For example, of the four reservoirs that have had restoration stockings (Eufaula, Texoma, Oologah, and Kaw), only Kaw and Oologah lakes have evidence of natural reproduction (Schwemm et al. 2015, J. Schooley personal communication). How availability of spawning substrate in tributaries to these reservoirs has affected these results is unknown.

Historically, mapping rivers on a scale adequate to assess the availability of spawning substrates in relation to restoration success of a migratory species would have been unfeasible due to monetary and time constraints (Kaeser and Litts 2010). Previous attempts to locate spawning substrates were limited to visual identification in discrete locations thought to be used by Paddlefish, which lack a broader understanding about abundance throughout the system. These typically involved using radiotelemetry to track fish and sample substrates where congregations of fish were found (Paukert and Fisher 2001; Firehammer and Scarnecchia 2006, Schwinghammer et al. 2018). While successful, the results of this approach only provided locations of substrate at points and did not quantify the amount of substrate, especially outside of tracked fish locations. However, the use of geographic information systems (GIS), global positioning systems (GPS) and remote sensing devices adept at mapping lotic habitat at large spatial scales has accelerated in the past decade (Kaeser and Litts 2010; Casado et al. 2015;

Walker and Alford 2016; Schooley and Neely 2018). In particular, the use of side-scan sonar (SSS) has become a common method for mapping navigable streams and rivers on a broad scale in part because of low-cost, recreational grade units becoming available along with software from a variety of vendors in secondary markets (Kaeser and Litts, 2010, Buscombe 2017).

Side-scan sonar, a form of hydroacoustic remote sensing, was originally developed for seafloor mapping and identification of objects of interest in vast deep water environments (Fish and Carr 1990). Since that time, significant advances in SS have made it an invaluable tool in contemporary inland fisheries science applied to shallow water environments (Meadows 2013; Buscombe 2017; Vine et al. 2019). Typically SSS is composed of three parts; a head unit for recording and visualization of sonar data, a data transmission cable, and a subsurface transducer capable of transmitting and receiving acoustic pulses. The transmission and reception of these acoustic pulses is interpreted by the head unit displaying high resolution acoustic imagery, of which it is possible to discriminate differences in substrate composition (Kaeser and Litts 2010; Buscombe et al. 2017). This technology has been used extensively in shallow water fluvial (Kaeser and Litts 2010), lacustrine (Richter et al. 2016) and estuarine environments (McLarty et al. 2020) and is capable of mapping an area encompassing thousands of km² a day, primarily for identification of benthic habitats (Buscombe et al 2017).

Advances in remote sensing using aerial imagery (AI), more commonly used for terrestrial applications, have also recently been used for the identification of instream habitat and substrates (Casado et al. 2015; Arif et al. 2017). Using either supervised or unsupervised classification of high resolution AI, pixels can be assigned to different classes, such as substrate type, based on spectral values from images using various statistical analyses (Lillesand and Kiefer 1994; Arif et al. 2017).

Identifying spawning substrates in tributaries of reservoirs where Paddlefish occur or might be stocked can provide valuable insight for restoration stocking. Moreover, the different characteristics among the systems make them variously amenable to substrate mapping by sonar and aerial image interpretation, allowing for on-the-ground tests for the utility of these tools. Using these remote sensing tools, our objectives were to (1) estimate the quantity of suitable spawning substrates (gravel/cobble, boulder, bedrock) in the first 50-km of river upstream of these study reservoirs and (2) relate the quantity of suitable spawning substrates to Paddlefish persistence status in their respective reservoir settings.

METHODS

Study Area

The focus of this research was six river-reservoir systems in the Arkansas River and Red River drainages of Oklahoma (Figure 1; Table 1-2) where Paddlefish occur, have been stocked, and or potential locations for stocking (Table 3). These river-reservoir systems differ in size, location, and likely in terms of amount of suitable spawning substrate for Paddlefish. To assess these multiple systems in a relatively short period, we surveyed the first 50-km of river habitat upstream of the river-reservoir interface.

Kaw Lake, Arkansas and Walnut rivers — Kaw Lake is the most upstream reservoir on the Arkansas River in Oklahoma and is managed as a hydropower facility. Throughout the early to mid-1990's Kaw Lake was stocked with 48,000 Paddlefish and in 2017 evidence of natural reproduction was found with state biologists confirming multiple reports of anglers catching juvenile Paddlefish in cast nets (J. Schooley, ODWC, personal communication). A lowhead dam, approximately 129 km upstream of the reservoir on the Arkansas River exists near Wichita, KS, likely limits upstream migration of Paddlefish except during extreme high flows and Paddlefish have been snagged below the dam (Neely et al. 2015; Pennock et al. 2018). The Walnut River is a tributary of the Arkansas River, located near Arkansas City, KS, approximately 27 km upstream of Kaw Lake. Tunnel Mill Dam, a migration barrier in the Walnut River, is located approximately 41 km upriver from the confluence and has been previously open to Paddlefish snagging (Neely et al. 2015).

Keystone Lake, Arkansas and Cimarron rivers — Keystone Lake is located downstream of Kaw Lake, at the confluence of the Arkansas and Cimarron rivers in northcentral Oklahoma. The lake has no history of being stocked with Paddlefish, but has a self-sustaining population

that supports recreational harvest and holds the current state and world records (ODWC 2021). The Cimarron River is a largely unimpeded prairie river that flows east from its origins in New Mexico, and has large variations in flow dependent on precipitation. Furthermore, the Cimarron River has high concentrations of dissolved and suspended sediments, and has a dominant substrate of sand (Reash 1990; Paukert and Fisher 2001). The Arkansas River flowing into Keystone Lake is regulated by discharge from upstream Kaw Dam, with a mean annual discharge of 175.2 cms and is the largest river under study. The Arkansas River in this stretch is a wide and shallow braided prairie river, with a substrate dominated by sand.

Eufaula Lake, North Canadian and Canadian rivers — Lake Eufaula is the second largest lake in Oklahoma by water volume, and the largest by surface area at 42,690-ha. The lake was created by damming the Canadian River just before its confluence with the Arkansas River, and is near the town of Eufaula in eastern Oklahoma. Over 200,000 Paddlefish were stocked in Lake Eufaula between 2007 and 2017 and a small-scale snag fishery was evident by 2015 (Jager and Schooley 2016). On the northern end of the lake, the North Canadian River flows from the west with a mean annual discharge of 26.0 cms. The North Canadian River is illustrative of typical prairie rivers, being shallow, braided and having predominantly sand substrate. On the southern end of the lake, the Canadian River (also known as South Canadian River) is the contributing tributary and exhibits high amounts of suspended sediments and a predominately sand substrate (Pigg et al. 1999). The Canadian River is also a typical prairie river, being wide, shallow and braided with seasonal fluctuations in flows, averaging 48.5 cms discharge.

Lake Tenkiller, Illinois River — Lake Tenkiller is an impoundment of the Illinois River located in eastern Oklahoma. Lake Tenkiller has not been stocked with Paddlefish, but historic populations have been noted in the Illinois River above the lake prior to impoundment (Riggs

and Moore 1949) and is under consideration by ODWC for stocking. The Illinois River is a shallow Ozark river with a predominant substrate of gravel and cobble, and a mean annual discharge of 35.3 cms. The Illinois River flows unimpeded 101 km from the state line at Arkansas through the Ozark Mountain ecoregion into the northern part of Tenkiller Lake (Harmel et al. 1999).

Oologah Lake, Verdigris River — Oologah Lake was created by damming the Verdigris River just east of Oologah, Oklahoma. Stocking of over 30,000 Paddlefish occurred from 1995-2000 and data acquired from the ODWC Paddlefish Research Center and ODWC e-check harvest indicate that over 100 fish have been harvested from the Verdigris river and its tributaries since 2014 (J. Schooley unpublished data). Paddlefish population monitoring surveys were conducted by ODWC in 2013 and 2014, of which 99.7% of fish collected did not have coded wire tags, indicating they were the product of natural reproduction (J. Schooley unpublished data). The Verdigris River is a deep, channelized river with well-defined and stable banks, and the riverbed comprised of rock, shale and bedrock substrate (Wallen 1956). Just above the confluence with Oologah Lake, the Verdigris River has a mean annual discharge of 85.7 cms, and is the second largest river under study. The Verdigris River is free-flowing for approximately 245 river km from Toronto Lake near Toronto, Kansas to Oologah Lake and is characterized by a series of wide bends connected by straight segments (Wallen 1956).

Lake Texoma, Red and Washita rivers — Lake Texoma is the largest lake in Oklahoma by water volume, and was created by impounding its two tributaries, the Red and Washita rivers. Stocking occurred from 1999 to 2007, although no natural reproduction was ever reported and high annual mortality was evident (Patterson 2009). However, Paddlefish harvest was reported in the area in 2015, eight years after the last stocking event, although it is unclear if these fish were

harvested from Lake Texoma or in the Red River below Denison Dam (Jager and Schooley 2016). The Red River flows across the modern Oklahoma-Texas border, and is shallow, braided and wide with a dominate substrate of mud and sand (USDA Field Advisory Committee 1977). The mean annual discharge of the Red River is 89.5 cms but is highly variable throughout the season. The Washita River originates in the Texas panhandle and, in the 50-km segment above the lake, is channelized with steep banks and the dominant substrates of mud and sand. (Matthews 1988; Patterson 2009).

Remote Sensing for Habitat Mapping

Side-Scan Sonar Data Collection –We mapped eight of ten reservoir tributaries using a Humminbird MEGA SI sonar unit (Figure 1). A fixed GPS antenna was mounted directly above a bow-mounted transducer operating at a frequency of 1.2 MHz to collect georeferenced sonar data, using two to three transects in the downstream direction at speed of 4.8 km/h – 12 km/h. The number of transects varied depending on river width in an attempt to provide bank-to-bank coverage. Data were collected during high discharge events at the 80th percentile of mean daily flow or higher on a 50 km stretch of river above the river- reservoir interface to quantify substrate available to Paddlefish during spawning.

Side-Scan Sonar Imagery Analysis – SSS imagery was imported into ReefMaster 2.0 software to blend, enhance and analyze data from SSS transects. Transects from the same river were merged in ReefMaster 2.0 using the mosaic tool to create one contiguous image of SSS data and substrate identified by particle size (i.e., silt/sand, gravel, cobble, boulder, bedrock; Wentworth 1922) was classified based on the image texture, tone, shape and pattern from the SSS imagery (Kaeser and Litts 2010; Figure 2). Substrates identified as gravel, cobble, boulder and bedrock were all considered suitable, others were considered unsuitable (Crance 1987; Jennings and Zigler 2000). Polygons were constructed around substrate types in Reefmaster 2.0, exported to ArcMap 10.8, and summarized by area (ha).

Identification of the surveyed area differed depending on the availability of bank-to-bank coverage. The preferred method to delineate the surveyed area was to identify the bank using the SSS imagery. In rivers where bank-to-bank coverage was possible and the bank could be identified from SSS imagery, we manually added points in ArcMap 10.8 corresponding to the bank, spaced approximately 2.5 m apart (Figure 3). Points were then linked to create a polygon representing the extent of surveyed area. In some rivers, bank-to-bank coverage could not be fully obtained with SSS, often because the river was too shallow even at high flow, obscuring the location of river bank from the sonar. In these cases, a buffer was applied from the midline of the transect (Figure 4) to delineate the survey area, where the buffer distance was the average of the distance from 3 points (beginning, middle and end of transect) along the transect path perpendicular to the furthest identifiable area. This buffer method was used to standardize the identification of the area in which side-scan sonar could identify substrates, which were largely unsuitable.

Supervised Classification of Aerial Imagery – Supervised classification is a technique using quantitative analysis of pixels in remote sensing imagery of known composition to classify pixels of unknown composition in the study area extent. Automatically categorizing pixels based on their spectral values, and transforming them into forms of a classified group in the raster is the main objective of applying supervised classification (Lillesand and Kiefer 1994). The maximum likelihood classification, a statistical method of supervised classification, was used to analyze remote sensing imagery. This method extracts spectral values from raster bands that comprise imagery and computes the likelihood of group membership to training site classes. This method also provides a confidence ranking based on the likelihood that it belongs to the class it was assigned, which was used to remove pixels from the analysis below a specified confidence ranking, improving accuracy.

For the Canadian and Illinois rivers, we relied on supervised classification via the maximum likelihood method of aerial imagery (AI) at low flows as the sole substrate classification technique (Figure 5). This method was employed because hydrology and limited access to these rivers resulted in mean sampling windows of 1.26 and 2.6 days for the Canadian and Illinois rivers respectively (Figure 6).

While this method allowed for classification of substrates that would be inundated at high flow and potentially accessible to Paddlefish for spawning, it precluded classification of submerged substrate at low flow that was not visible under standing water at the time of the photography. As a result, this method did not estimate the entirety of submerged substrates, but it allowed for estimation of a majority of substrates that would be available at high flow. Additionally, in the Arkansas River above Keystone Lake, the Arkansas River above Kaw Lake, and the North Canadian River, where SSS could not capture the entire width of the river and the bank, AI was used to supplement SSS substrate mapping. When AI and SSS data overlapped, SSS took precedence in the identification of substrate.

Aerial imagery for substrate classification was obtained from NAIP (National Agriculture Imagery Program; https://gdg.sc.egov.usda.gov/GDGHome_DirectDownload.aspx). Imagery produced by NAIP is captured at 1m x 1m pixel resolution of red, green and blue spectral bands during the agricultural growing season and states are typically surveyed on a three-year rotation. Because imagery is acquired in the growing season, images usually coexist with low discharge in Oklahoma rivers and is ideal for mapping exposed substrates. We first acquired imagery to determine years when the river of interest was in a period of low discharge to map substrates when they were exposed. Next, we acquired imagery at high discharge to determine the extent of inundation for mapping substrates when they would be submerged and available for use by spawning Paddlefish (Table 4). For imagery at high discharge, we created a polygon of water with a maximum likelihood classification in ArcMap 10.8 software (Figure 5). If no imagery during high discharges was available, a polygon was manually created around the presumptive flooded channel observable in low flow imagery (Figure 5). From low flow imagery, we then classified areas of exposed substrates within the flooded extent polygons. Exposed substrates were classified using 10 to 30 training sites of known substrates and the maximum likelihood classification tool in ArcGIS 10.8 software was used to then classify and quantify all exposed substrate types (Table 5).

The amount of substrate classes used for analysis of aerial imagery varied among rivers (Table 5). When possible, one class of exposed substrate was used to classify exposed substrates using a reject fraction to avoid the inclusion of other classes of ground cover. In other rivers, particularly the Canadian

and North Canadian rivers, multiple classes were used to increase the reliability of classifying exposed substrates because of similarities of spectral values in pixels. When multiple classes were used, only those relevant to Paddlefish spawning were included in ground-truthing and substrate quantification.

Ground-Truthing Assessment – To assess the accuracy of our classified substrate maps, 400 points were randomly placed proportionally within classified substrate type polygons using the Random Point Generator tool in ArcMap 10.8. Points were placed with a 3-m buffer to ensure sampling of the correct polygon (Kaeser and Litts 2010). When the overall percentage of substrate was $\leq 1.0\%$, that class was assigned two points per habitat patch for accuracy checking. For field verification, surveyors navigated to points via kayak and hand held GPS units and visually identified the substrate. When points were vegetated, the substrate underneath was assessed. For submerged points, a ponar grab was used to identify substrate. In rivers where the primary substrate identification method was AI or gaps in SSS imagery (Canadian, Illinois and Cimarron rivers), areas of potentially suitable substrates for Paddlefish spawning not classified during remote sensing (e.g., bedrock) were identified and delineated with beginning and end points for inclusion in the final substrate maps. For these areas, a 1-m buffer, which was the resolution of the NAIP AI, around the line connecting the beginning and end point was used to estimate area.

To estimate substrate classification accuracy, individual confusion matrices were created for each river depending on substrates identified (Kaeser and Litts 2010). Using these confusion matrices we calculated three accuracy statistics to assess our maps: overall accuracy, producer's accuracy and user's accuracy. Overall accuracy represents the proportion of correctly classified points identified during ground truthing surveys and provides a general understanding of map accuracy. Producer's accuracy describes the map maker's ability to correctly identify substrates, this translates to the strength of our supervised classification or our ability to discern different substrates from SSS imagery. Lastly, user's accuracy describes the proportion of classified areas on the map that are correct, describing how reliable a substrate will represent what it is classified as for those using the map.

RESULTS

Spawning Substrate Identification

Across all 10 river systems, we classified substrates in 4,550 ha of river, with approximately equal amounts estimated with SSS and AI, but these varied within rivers (Table 6). In eight river systems, SSS comprised the majority of the classification area, with 192 transects representing 2,737 ha of area. In five river systems, AI comprised 1,813 ha of classification area, supplementing SSS imagery in three rivers (Arkansas River above Kaw and Keystone lakes, North Canadian River) and the sole method for two (Canadian and Illinois rivers). In the Cimarron and Canadian rivers, where areas of suitable substrate were not surveyed by SSS or classified by AI, *in-situ* measurements of substrate during ground-truthing were included in the total area of suitable substrates. From these classifications, only the Verdigris, Illinois and Walnut rivers had proportional suitable substrate areas exceeding 40%; the remaining rivers had minimal (<1.5%) amounts of suitable spawning substrate in the study reach, mostly being comprised of unsuitable sand (Table 7 and 8).

Substrate classification accuracy varied among SSS and AI methodology, although accuracies greater than 90% were common. Classification of AI resulted in accuracies greater than 90% for all rivers except for the Arkansas River above Keystone Lake (87.9%; Table 7), although this method was only capable of quantifying large patches of homogenous substrates. Classification of SSS imagery was less accurate when distinguishing between suitable and unsuitable, ranging from 25% to 98.9%, but was adept at identifying multiple categories of substrates at finer scales (Table 9). For example, classification of substrates using AI could only identify one category of exposed substrates, whereas SSS could identify all categories of submerged substrates.

All but three river substrate maps, which incorporate both SSS and AI when available, had overall accuracies exceeding 90% (Tables 12 to 21). The lowest accuracies came from the Arkansas River above Keystone (86.9%), the Verdigris River (65.8%) and the Walnut River (57.5%). Producer's

accuracy ranged from 11% to 98.2% with unsuitable substrates exhibiting the highest levels (83.6%-99.2%). For suitable categories, producer's accuracies were best for boulder (43.2%-84.7%), followed by cobble/gravel (20%-59.4%), and bedrock (0%-28%). User's accuracy ranged from 0% to 98.3% among substrate classes in all rivers with cobble/gravel exhibiting the highest user accuracy (74.3%-96.7%) followed by unsuitable types (62.7%-98.3%), boulder (20%-81.4%) and bedrock (0%-18.2%).

Arkansas River, Kaw Lake – Using a combination of SSS and AI, we mapped a total of 734 ha of substrate, of which 46% was identified by AI and the remainder by SSS. Potentially suitable substrate represented 1% of total area and was comprised of mostly boulder and some cobble. All suitable substrates identified during mapping were located on the nearshore locations of the river (Figure 7.1-7.8). Overall accuracy of the substrate map created was 93.5% with high accuracies identifying boulder and unsuitable substrates (n = 356, Table 12). An additional 17 points of cobble/gravel were identified during ground truthing, suggesting underestimation of smaller suitable substrates not classified by AI or SSS but was not further quantified.

Walnut River, Kaw Lake – In total, 32.9 ha of substrate were mapped in 5 km of the Walnut River. Mapping was restricted to the lower 5 km of river to the Arkansas River confluence due to water access laws in Kansas. However, suitable substrates were common, comprising 56% of the area mapped, including cobble/gravel types in the main channel (Figure 7.5). Ground-truthing was limited to 40 points because of the short distance surveyed and overall accuracy was the lowest of any river surveyed at 57.5% (n = 40, Table 13). Low accuracy can be attributed to misclassification of suitable substrates as unsuitable, resulting in a 47% classification accuracy of unsuitable substrates. Additionally, accuracy of cobble/gravel substrates was 66.7% with the majority of misclassifications being larger suitable substrates. The Walnut River had the largest proportion of suitable substrates surveyed, which were

underestimated, indicating a larger disparity between suitable and unsuitable substrates than identified in the substrate map.

Arkansas River, Keystone Lake – In the Arkansas River above Keystone Lake, 48% of the 1,097 ha of the area was classified using SSS and 52% by AI. In total, potentially suitable substrate for spawning by Paddlefish represented 1% of mapped substrate and was predominantly boulder (Table 7). However, we did locate an additional 31 points of gravel/cobble during ground-truthing surveys that were not identified through either classification method, increasing the total amount of suitable substrate available, but we did not quantify the extent of these habitats. Overall accuracy of the substrate map created for this river was 86.9% (n = 381, Table 14), with the majority of the points inaccurately classified as unsuitable. In general, except for gravel/cobble areas identified during ground-truthing surveys, hard substrates tended to occur near the bank on outside bends of the rivers (Figure 8.1-8.7).

Cimarron River, Keystone Lake – The Cimarron River was mapped using only SSS, which amounted to 323.1 ha of substrate. The only potentially suitable substrate found was boulder (1% of total) and all but two of these patches occurred near banks on outside bends of the river. The two patches of deep water, in-channel boulder habitat occurred between RKM 22 and 24 (Figure 8.10), this was the only location large suitable substrates were found in the midchannel of a prairie river we surveyed. Overall accuracy of the substrate map was 94.6% (n = 373, Table 15), which was consistent with other braided prairie rivers surveyed. Of the 288 ground-truthing points placed in unsuitable substrate polygons, 9 were boulder and 3 were bedrock, suggesting a slight underestimate of suitable substrates. Throughout, no gravel/cobble was found in SSS transects or in ground-truthing surveys.

North Canadian River, Lake Eufaula – The North Canadian River was surveyed by a combination of SSS (76.3%) and AI (23.7%), for a total area of 364.5 hectares. Nearly all (98.8%) of the area surveyed was composed of unsuitable sand and mud; the remaining 1.2% was classified as boulder. Areas of suitable substrate that were identified were consistently found in deeper areas of the river

concentrated on the outside of river bends (Figure 9.1-9.6). The overall accuracy of the substrate map for this river was 97.9% (n = 373, Table 16), which was the highest of any river surveyed.

Canadian River, Lake Eufaula – The Canadian River was surveyed using only classification of AI, which identified 767.9 ha of exposed sand substrates. Ground-truthing surveys identified a 93.5% overall accuracy of exposed substrates (n = 323, Table 17). Most ground-truth points not identified as sand were detritus or mud, which still classify as unsuitable for spawning by Paddlefish. During ground-truthing surveys, nine patches of suitable boulder substrate, totaling 0.0681 ha, were found, all on the outside bends of the river (Figure 9.7-9.14).

Illinois River, Lake Tenkiller – Classification of 142 ha of exposed substrates from AI in the Illinois River resulted in 96.7% accuracy (n = 335, Table 18) in identifying the predominant class of gravel/cobble substrate. Of the remaining 3.3%, half was identified as unsuitable (sand), and the other half as suitable (boulder).

Verdigris River, Oologah Lake – The Verdigris River was surveyed by 28 transects of SSS, and had the highest diversity of substrates of all the study rivers. In total, 344.7 ha of area was surveyed and 46% was classified as suitable, with substrate types consisting of gravel/cobble, boulder, and bedrock. The dominant substrate class was gravel/cobble, which represented 37% of the total area surveyed. The remaining 54% of area was classified as unsuitable, consisting of mud, clay or silt. Overall ground-truthing accuracy in this river was 65.8% (n = 392, Table 19), but this was largely attributed to the diversity of the substrates. Most ground truthing error resulted from suitable substrates that were classified as unsuitable substrates (n = 79, Table 19), suggesting underestimation of suitable substrates. Most cobble/gravel substrates were found in the mid-channel of the river, whereas larger substrates like boulder were found in the near bank areas of the river (Figure 11.1-11.5).

Washita River, Lake Texoma – We surveyed 243.3 ha of the Washita River using SSS, the smallest area of all rivers surveyed due to a blockage of access to the upper 10 km stretch. Only 0.5% of

the area was classified as suitable substrate, which consisted of cobble/gravel that was concentrated near the beginning of the study area (0.2% of total), and boulder dispersed throughout (0.3% of total; Figure 12.1-12.6). The majority of unsuitable substrate was clay, silt and sand. Ground-truthing accuracy was 93.9% (n = 393, Table 20).

Red River, Lake Texoma – The Red River was surveyed using only SSS and the 504.4 ha examined had a composition of 99% unsuitable substrates, mostly sand. Boulder substrates represented 1% of the total area and were evenly distributed throughout the length of the study area, but only on the banks, never mid channel (Figure 12.7-12.13). Substrate classification accuracy was 94.6% (n=388, Table 21). Seven points were identified as suitable substrates, cobble/gravel and bedrock, through ground truthing that were not found using SSS.

DISCUSSION

Mapping substrates in the first 50 km of river upstream of river-reservoir interfaces allowed us to evaluate its potential role in successful restoration efforts. However, we had to tailor our mapping methods in our 10 study rivers because of the large variation in hydrology and morphology among rivers. Accuracies were highest in rivers that were largely homogenous where we were limited to solely using AI. Additionally, in rivers that had largely homogeneous substrates, suitable substrate categories identified by SSS often had the lowest classification accuracy. Generally, these two conditions occurred in prairie rivers, which were shallow and wide with sand substrates. These systems were not as conducive to SSS mapping because bank-to-bank coverage was rarely achievable. Conversely, rivers that were more channelized (Walnut, Verdigris and Washita) provided better coverage with SSS because of narrow widths and more substantial depths.

Coverage varied among rivers depending on the morphology and hydrology of each river, but was not quantified. In general, however, the wide and shallow prairie rivers would have required more than the three transects to achieve complete bank-to-bank coverage. In particular, the width of these systems, in relation to their depth, coupled with small sampling windows suitable for boat navigation, made bank-to-bank coverage by SSS extremely difficult. Adding classification by AI improved coverage, but was limited to areas not inundated by water, resulting in gaps still remaining. However, an increased effort to achieve complete coverage would probably not provide more insight into the abundance of suitable substrates. Side-scan sonar and classification of AI did not identify any suitable substrates smaller than boulder in these rivers, and ground-truthing surveys often only found suitable substrates in nearshore areas that could not be identified by remote sensing. For example, the Arkansas River above Keystone

and Kaw lakes contained some suitable substrates smaller than boulder (i.e., gravel/cobble) identified through ground-truthing that was obscured in SSS imagery, emphasizing the need for on-the-ground surveys.

In general, availability of suitable spawning substrate coincided with Paddlefish population status. Three of the river-reservoir systems in this study had evidence of natural reproduction (Kaw, Keystone, Oologah) and suitable substrate abundance in tributaries sometimes exceeded 40%, but this was more common in the Walnut and Verdigris rivers above Kaw Lake and Oologah Lake, respectively. In Keystone Lake, suitable substrates were scarce in both of its tributaries. However, we did document gravel/cobble substrates in the Arkansas River in the first 50 km above the reservoir during ground-truthing surveys, suggesting that our estimates of the amount of suitable spawning substrates based on SSS and AI were underestimated. Moreover, we documented likely suitable substrates in the Cimarron River that were located in deeper, mid-channel areas. For Paddlefish in Keystone Lake, the ability to use these two rivers as a source for successful spawning may help ensure population stability. Furthermore, we limited our survey to the first 50 km of river above the reservoir and additional areas of suitable substrate patches much further upstream likely exist. For example, this portion of the Arkansas River from the reservoir upstream to Kaw Dam is 176 km and Keystone Lake Paddlefish are known to regularly migrate its full extent in addition to the Salt Fork of the Arkansas River and patches of gravel/cobble have been documented previously (Paukert and Fisher 2001). Moreover, the tailwaters of Kaw Dam are scoured to bedrock and is likely conducive for spawning by Paddlefish (Parsley et al. 1993; Bruch and Binkowski 2002; Duncan et al. 2004). Scoured areas below dams in the tailwater would provide consistent spawning areas

and help explain the self-sustaining population of a river-reservoir system with scarce amounts of suitable substrates in its tributaries.

The influence of regional geology may also play a key role affecting Paddlefish reproduction and population stability in Oklahoma. For instance, Kaw and Oologah lakes were two systems we considered for this study and both had at least one tributary that had large proportions (>40%) of suitable substrates. Moreover, Grand Lake O' the Cherokees is another reservoir in the area with a stable Paddlefish population, although we did not study this system in this project. However, a multitude of other research has been conducted on this population and the Neosho River and Spring River tributaries are known to have large proportions of suitable substrates and support Paddlefish reproduction (Schooley and Neely 2018). The three watersheds of these three adjacent reservoir systems, including the Walnut River, Verdigris River, and Neosho River have similar alluvial deposits of chert gravel overlaying bedrock (Aber 1992; Aber 1997). Abundance of suitable substrates, likely as a result of the regional geology, in these rivers helps explain the successful natural reproduction that has been documented in these systems.

Lakes Eufaula and Texoma, where restoration efforts have taken place, have some tributaries that mirror the substrate composition of tributaries in reservoirs with sustainable populations of Paddlefish, although no evidence of natural reproduction has been found in either lake. This suggests other factors such as genetics, predation, food availability and hydrology may also be important in reestablishing a self-sustaining Paddlefish population (Paukert 2001; Parken and Scarnecchia 2002; Mero et al. 2011; Schooley and Neely 2018). Successful restoration in reservoirs hinges on the survival of stocked fish to sexual maturity, subsequent spawning by the stocked population, and survival of resultant progeny to adulthood. Paddlefish stocked in Lake Texoma were of Grand Lake origin, which differ genetically from the Red River population that

historically occupied the region (Schwemm et al. 2015). Fish from stocked from outside sources are less genetically fit (Ward 2006), and this could have affected survival in Lake Texoma, which is on the fringe of Paddlefish's historic range with extremes in temperature and salinity. Additionally, mortality of stocked Paddlefish is also affected by the abundance of large predators (Parken and Scarnecchia 2002; Mero et al 2011). In Lake Texoma, where there is an abundance of Striped Bass (*Morone saxatilis*), predation of stocked Paddlefish was considered a potential contribution to the failure of restoration efforts (Patterson 2009). Moreover, Paddlefish are indiscriminate filter feeders for the majority of their life history, and low densities of Paddlefish forage may lead to increased energetic demands, which could result in limited survival of stocked fish and reduced growth or body condition of surviving fish (Blackwell et al. 1995; Moore and Cotner 1998; Chipps et al. 2009). Another factor effecting Paddlefish foraging may be reservoir tributary turbidity. During early life stages, Paddlefish larvae are visual zooplanktivores. High turbidities in rearing habitat of reservoir tributaries could lead to decreased success in foraging and poor recruitment (Eachus 2021). Lastly, while there are no exact metrics of river hydrology that can be used as a threshold for successful Paddlefish spawning, increases in spring discharges need to accommodate several phases of the Paddlefish reproductive biology including: upstream migration, spawning, egg incubation and hatching (Schooley and Neely 2018). Reproductive success may be thwarted if characteristics of tributary hydrology such as high discharge frequency and high discharge duration are not suitable for Paddlefish spawning.

Lake Tenkiller, identified as a potential restoration site, has conflicting attributes that make identifying its potential restoration outcome challenging. The Illinois River, Lake Tenkiller's biggest tributary, had a composition of largely homogeneous cobble and gravel

suitable for Paddlefish spawning. However, hatching success could be hampered due to hydrologic volatility. The Illinois River is flashy, which is not conducive to spawning migrations or egg incubation and hatching (Schooley and Neely 2018). Moreover, the zooplankton community may limit the survival of stocked Paddlefish (Blackwell et al. 1995; Moore and Cotner 1998; Parken and Scarnecchia 2002; Chipps et al. 2009; Mero et al 2011). In a recent study of the zooplankton community, Lake Tenkiller had one of the lowest abundances among reservoirs with Paddlefish populations in Oklahoma (Eachus 2021). As a result, the Illinois River may contain suitable substrate to support Paddlefish spawning, but hydrology and zooplankton abundance may hinder a self-sustaining population.

Future research to better understand restoration success and the reproductive dynamics of Paddlefish could provide more accurate forecasts of restoration outcomes. For example, efforts to determine the location of spawning can give a more definite answer to what areas may be conducive to successful spawning. This information could be provided by telemetry or microchemistry analyses of dentary bones to identify natal areas and help determine the contribution of various river systems and the effects of hydrology. Additionally, future mapping could identify spawning habitat in the known migratory range of Paddlefish. Identifying more precisely what contributes to successful spawning by Paddlefish in Oklahoma reservoirs with known recruiting populations will help better guide restoration efforts in other systems.

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TABLES AND FIGURES

Table 1. Physical size characteristics of reservoirs in Oklahoma where estimates of suitable spawning substrate quantity for Paddlefish were acquired in connected tributaries. Measurements are based on water elevations in the reservoir at conservation pool level.

Reservoir	Volume (m ³ x 10 ⁶)	Surface Area (ha)	Max Depth (m)	Year Impounded
Kaw	447.1	6,895	22.7	1976
Keystone	532.8	9,554	22.3	1968
Oologah	563.9	11,920	21.9	1963
Tenkiller	824.2	5,220	40.5	1953
Eufaula	2,707.3	42,690	27.5	1964
Texoma	3,022.5	36,000	43.3	1944

Table 2. Hydrologic characteristics of tributary rivers to Oklahoma reservoirs where surveys of potentially suitable spawning substrate for Paddlefish were carried out in 2019-2021. Discharge values were calculated using 2011 – 2020 water years from the respective USGS gage.

River	USGS Gage	Mean Annual Discharge (m ³ /s)	Median Discharge (m ³ /s)	80 th Percentile (m ³ /s)	Variability ¹	Watershed Area (km ²)
Arkansas Above Kaw	07146500	64.2	25.3	65.83	3.73	113,216
Walnut River	07147800	32.8	6.0	30.85	4.38	4,869
Arkansas Above Keystone	07152500	175.5	71.9	239.02	3.47	141,063
Cimarron	07161450	38.5	12.7	31.58	4.20	46,565
North Canadian	07242000	26.0	9.9	27.76	1.71	37,010
Canadian	07231500	48.5	11.1	46.7	0.72	72,395
Illinois	07196500	35.3	15.7	41.88	1.44	2,483
Verdigris	07171000	85.7	15.5	124.52	2.28	9,424
Washita	07331000	51.4	17.2	63.96	2.64	18,653
Red	07316000	89.5	19.7	90.56	3.07	79,725

¹Variability across annual flows calculated by subtracting the 10th percentile from the 90th percentile and divided by the median of the annual means.

Table 3. Stocking history of Paddlefish into six reservoirs in Oklahoma provided by Tishomingo National Fish Hatchery.

Reservoir	# Stocked	Stocking Years	Confirmed Natural Reproduction
Keystone	0	N/A	Yes
Kaw	48,000	1991-1995	Yes
Oologah	30,458	1995-2000	Yes
Eufaula	200,423	2007-2017	No
Texoma	119,520	1999-2007	No
Tenkiller	0	N/A	N/A

Table 4. Information about NAIP Imagery used for aerial imagery classification

River	Flow	NAIP Year	Flow (m ³ /s)	Percentile
Arkansas Kaw	High	N/A	N/A	N/A
	Low	2017	11-12	18 th – 19 th
Arkansas Keystone	High	2013	500 - 600	93 rd – 96 th
	Low	2017	18 – 21	22 nd – 24 th
North Canadian	High	N/A	N/A	N/A
	Low	2015	5.8 – 6.0	32 nd – 34 th
Canadian	High	N/A	N/A	N/A
	Low	2015	5.2 – 5.4	25 th – 26 th
Illinois	High	N/A	N/A	N/A
	Low	2017	7.3 – 7.9	17 th – 22 nd

Table 5. Specifics related to each supervised classification of NAIP imagery using the maximum likelihood technique in ArcMap 10.8.

River	# of Training Sites	Classes	# of Pixels in Training Sites	Reject Fraction
Arkansas Kaw	10	1	439,253	0.05
Arkansas Keystone	20	2	1,408,935	0.01
North Canadian	30	3	3,999,474	0.00
Canadian	30	3	959,019	0.01
Illinois	20	2	166,482	0.01

Table 6. Breakdown of the area surveyed by side-scan sonar and classification of aerial imagery for each river.

Rivers	Area Surveyed by Side-scan Sonar (ha)	Area Surveyed by Aerial Imagery (ha)	Total Area Surveyed (ha)
Arkansas Kaw	398.3	338.7	737
Walnut River	32.9	0	32.9
Arkansas Keystone	576.4	521.7	1,104.1
Cimarron	354.2	0	354.2
North Canadian	278.3	57.1	335.4
Canadian	0	767.9	767.9
Illinois	0	127.2	127.2
Verdigris	344.7	0	344.7
Washita	243.3	0	243.3
Red	504.5	0	504.5
Total	2,737.3	1,812.6	4,549.9

Table 7. Summary of supervised classification of substrates potentially suitable for spawning by Paddlefish from NAIP aerial imagery using the maximum likelihood method.

River	Exposed substrate classified area (ha)	Unsuitable ¹ (%)	Suitable ² (%)	Ground truthing Accuracy (%)
Arkansas Kaw	338.7	100	NA	
Arkansas Keystone	521.7	100	NA	87.9
North Canadian	86.2	100	NA	98.5
Canadian	767.9	100	NA	93.5
Illinois	142	NA	100	96.7

¹ Sand

² Cobble/gravel

Table 8. Percentage of presumably suitable (gravel/cobble, boulder and bedrock) and unsuitable (silt/sand/mud) substrate for Paddlefish in the 50-km of river upstream of the river-reservoir interface surveyed by side-scan sonar.

Rivers	Unsuitable %	Suitable %		
		Gravel/Cobble %	Boulder %	Bedrock %
Arkansas Kaw	99.3	<0.1	0.6	0
Walnut	46.2	44.7	6.8	2.3
Arkansas Keystone	99	0	<1	<0.1
Cimarron	99	0	1	0
North Canadian	98.5	0	1.5	0
Verdigris	54	37	6.25	2.75
Washita	99	<0.1	<1	0
Red	99	0	1	0

Table 9. Accuracy associated with predicting unsuitable or suitable substrate types drawn from individual river’s confusion matrices (Tables 11-20). Percentages indicate the proportion of points correctly identified as suitable or unsuitable compared to the total amount of points assigned to either substrate type.

River	Overall accuracy (%)	Unsuitable (%)	Suitable (%)
Arkansas Kaw	93.5	93.6	93.3
Walnut	57.5	66.7	93.3
Arkansas Keystone	86.9	88.5	68.8
Cimarron	94.6	95.8	82.2
North Canadian	97.9	98.6	80
Verdigris	65.8	62.7	69.4
Washita	93.9	97.9	25
Red	94.6	97.1	64.7

Table 10. Accuracy associated with predicting suitable substrates drawn from individual river’s confusion matrices. Percentages indicate how often we were correct when we identified a suitable substrate type i.e. if we predicted it was going to be cobble what percent of the time were we correct in that it was cobble and parallel for boulder and bedrock substrates. Columns with NA’s indicate that particular substrate was not identified in post processing of SSS imagery for its respective river.

River	Gravel/Cobble (%)	Boulder (%)	Bedrock (%)
Arkansas Kaw	50	94.8	NA
Walnut	66.7	100	0
Arkansas Keystone	NA	73.3	0
Cimarron	NA	81.4	100
North Canadian	NA	80	NA
Verdigris	74.3	64	18.2
Washita	75	20	NA
Red	NA	64.7	NA

Table 11. The total amount of suitable and unsuitable substrates found by either by SSS, AI or both for each reservoir tributary surveyed and the respective status of natural reproduction from their reservoirs.

Reservoir	Status	River	Suitable (ha)	Unsuitable (ha)
Kaw	Natural Reproduction	Arkansas River	2.62	731.9
		Walnut River	17.7*	15.2*
Keystone	Natural Reproduction	Arkansas River	5.2	1050.7
		Cimarron River	3.6	350.5
Eufaula	No evidence	North Canadian	4.0	330.5
		Canadian	0	767.9
Tenkiller	Potential Restoration	Illinois	127.2	
Oologah	Natural Reproduction	Verdigris	158.2	186.9
Texoma	No Evidence	Washita	1.2	242.1
		Red	4.74	499.7

*Only 5 km of Walnut River was surveyed

Table 12. Confusion matrix and associated statistics for the Arkansas River above Kaw Lake substrate map classification. The gray, diagonal cells of the matrix contain the correct classification of each substrate.

Predicted	Observed Substrate			Row Total	User's Accuracy
	Unsuitable	Cobble/Gravel	Boulder		
Unsuitable	277	17	2	296	93.6%
Cobble/Gravel	0	1	1	2	50%
Boulder	2	1	55	58	94.8%
Column Total	279	18	58	356	
Producer's Accuracy	99.2%	5.8%	94.8%		Overall Accuracy 93.5%

Table 13. Confusion matrix and associated statistics for the Walnut River substrate map classification.

The gray, diagonal cells of the matrix contain the correct classification of each substrate.

Predicted	Observed Substrate				Row Total	User's Accuracy
	Unsuitable	Cobble/Gravel	Boulder	Bedrock		
Unsuitable	8	7	2	0	17	47%
Cobble/Gravel	3	12	2	1	18	66.7%
Boulder	0	0	3	0	3	100%
Bedrock	1	0	1	0	2	0%
Column Total	12	19	8	2	40	
Producer's Accuracy	66.7%	63.2%	37.5%	0%		Overall Accuracy 57.5%

Table 14. Confusion matrix and associated statistics for the Arkansas River above Keystone Lake

substrate map classification. The gray, diagonal cells of the matrix contain the correct classification of each substrate.

Predicted	Observed Substrate				Row Total	User's Accuracy
	Unsuitable	Cobble/Gravel	Boulder	Bedrock		
Unsuitable	309	31	9	0	349	88.5%
Cobble/Gravel	NA	NA	NA	NA	NA	NA
Boulder	6	0	22	2	30	73.3%
Bedrock	0	0	2	0	2	0%
Column Total	315	31	33	2	381	
Producer's Accuracy	98.1%	NA	66.7%	0%		Overall Accuracy 86.9%

Table 15. Confusion matrix and associated statistics for the Cimarron River substrate map classification. The gray, diagonal cells of the matrix contain the correct classification of each substrate.

Predicted	Observed Substrate			Row Total	User's Accuracy
	Unsuitable	Boulder	Bedrock		
Unsuitable	321	9	3	333	96.3%
Boulder	6	30	4	43	69.7%
Column Total	327	39	7	373	
Producer's Accuracy	98.1%	76.9%	28.6%		Overall Accuracy 94.6%

Table 16. Confusion matrix and associated statistics for the North Canadian River substrate map classification. The gray, diagonal cells of the matrix contain the correct classification of each substrate.

Predicted	Observed Substrate		Row Total	User's Accuracy
	Unsuitable	Boulder		
Unsuitable	357	5	363	98.3%
Boulder	3	12	15	80%
Column Total	360	17	373	
Producer's Accuracy	99.2%	70.5%		Overall Accuracy 97.9%

Table 17. Confusion matrix and associated statistics for the Canadian River substrate map classification. The gray, diagonal cells of the matrix contain the correct classification of each substrate.

Predicted	Observed Substrate		Row Total	User's Accuracy
	Sand	Other		
Sand	302	21	323	93.5%
Column Total	302	21	323	
Producer's Accuracy	NA	NA		Overall Accuracy 93.5%

Table 18. Confusion matrix and associated statistics for the Illinois River substrate map classification. The gray, diagonal cells of the matrix contain the correct classification of each substrate.

Predicted	Observed Substrate			Row Total	User's Accuracy
	Gravel/Cobble	Boulder	Unsuitable		
Gravel/Cobble	324	6	5	335	96.7%
Column Total	324	6	5	335	
Producer's Accuracy	NA	NA	NA		Overall Accuracy 96.7%

Table 19. Confusion matrix and associated statistics for the Verdigris River substrate map classification. The gray, diagonal cells of the matrix contain the correct classification of each substrate.

Predicted	Observed Substrate				Row Total	User's Accuracy
	Unsuitable	Cobble/Gravel	Boulder	Bedrock		
Unsuitable	133	67	7	5	212	62.7%
Cobble/Gravel	17	107	14	6	144	74.3%
Boulder	2	4	16	3	25	64%
Bedrock	7	2	0	2	11	18.2%
Column Total	159	180	37	2	392	
Producer's Accuracy	83.6%	59.4	43.2%	11%		Overall Accuracy 65.8%

Table 20. Confusion matrix and associated statistics for the Washita substrate map classification. The gray, diagonal cells of the matrix contain the correct classification of each substrate.

Predicted	Observed Substrate			Row Total	User's Accuracy
	Unsuitable	Cobble/Gravel	Boulder		
Unsuitable	366	7	1	374	97.8%
Cobble/Gravel	1	3	0	4	75%
Boulder	10	5	3	15	20%
Column Total	377	15	4	393	
Producer's Accuracy	97.1%	20%	75%		Overall Accuracy 93.9%

Table 21. Confusion matrix and associated statistics for the Red River substrate map classification. The gray, diagonal cells of the matrix contain the correct classification of each substrate.

Predicted	Observed Substrate				Row Total	User's Accuracy
	Unsuitable	Boulder	Cobble/Gravel	Bedrock		
Unsuitable	345	5	3	1	354	97.4%
Boulder	9	22	0	3	34	64.7%
Column Total	354	27	3	4	388	
Producer's Accuracy	83.6%	43.2%	NA	NA		Overall Accuracy 94.6%

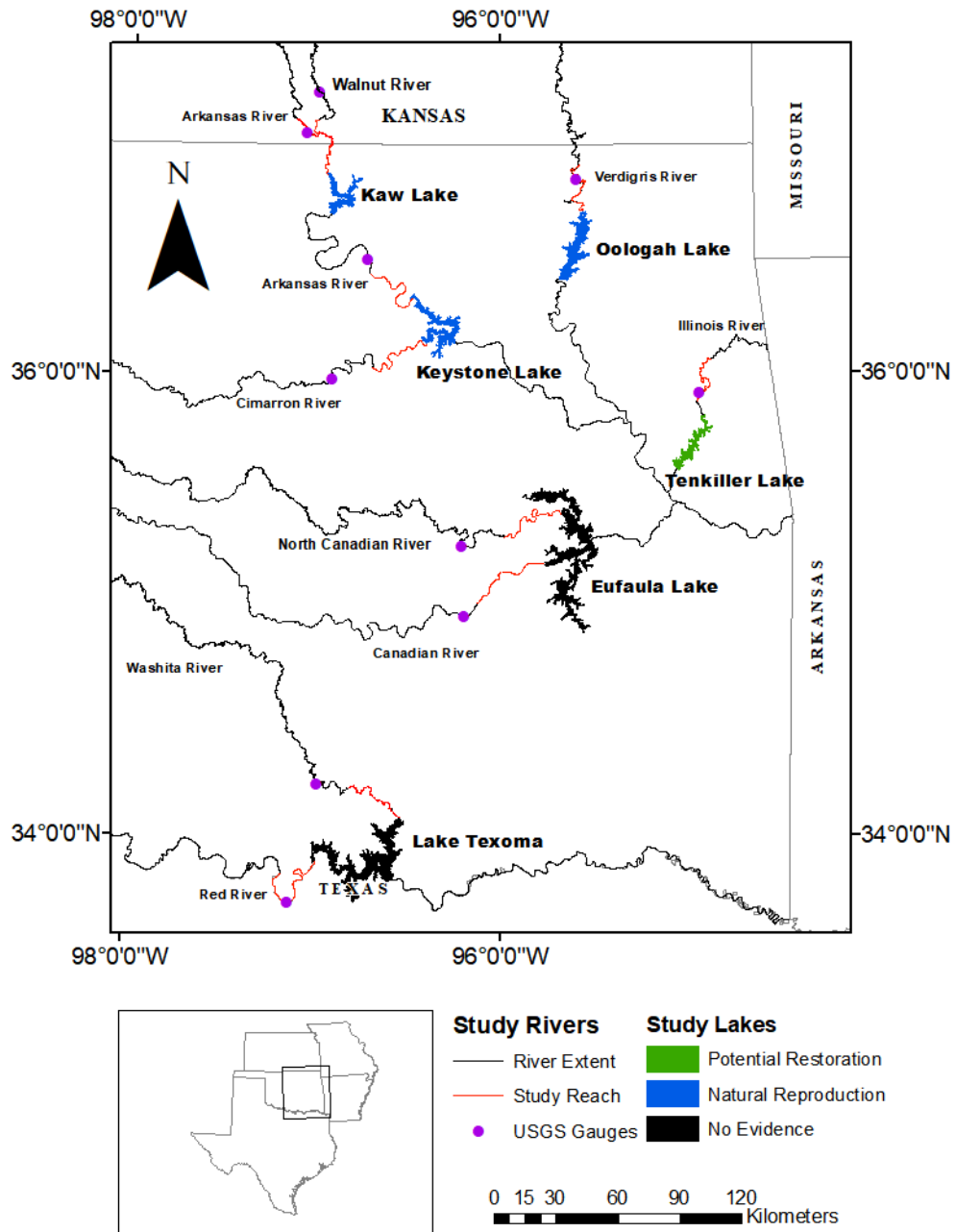


Figure 1. Map illustrating the 50 km study reaches (in red) and their associated river reservoir systems where remote sensing was used to estimate the amount of suitable spawning substrate for Paddlefish.

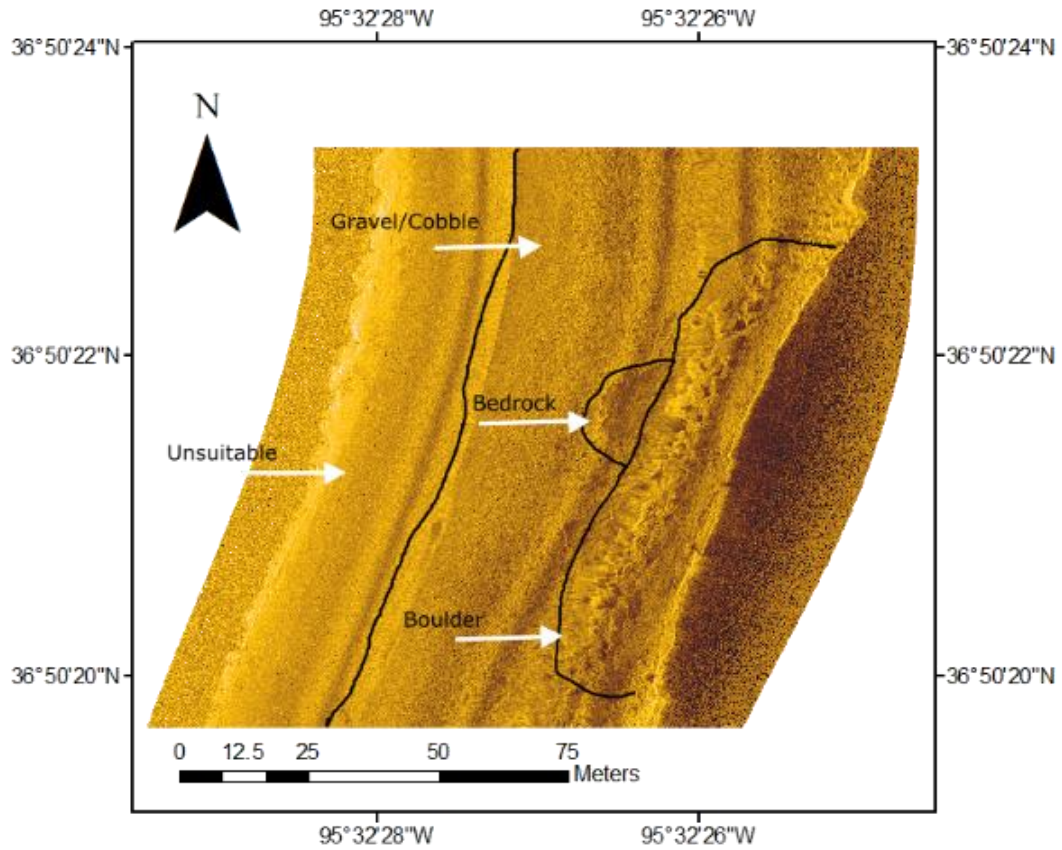


Figure 2. Sonar Imagery as viewed in ReefMaster v2.0 from the Verdigris River and annotated to highlight suitable and unsuitable substrate categories. Black lines have been drawn to outline the boundaries between the substrate categories, river banks can be identified as abrupt margins on either side with little variation in texture, tone or pattern parallel to the margin.

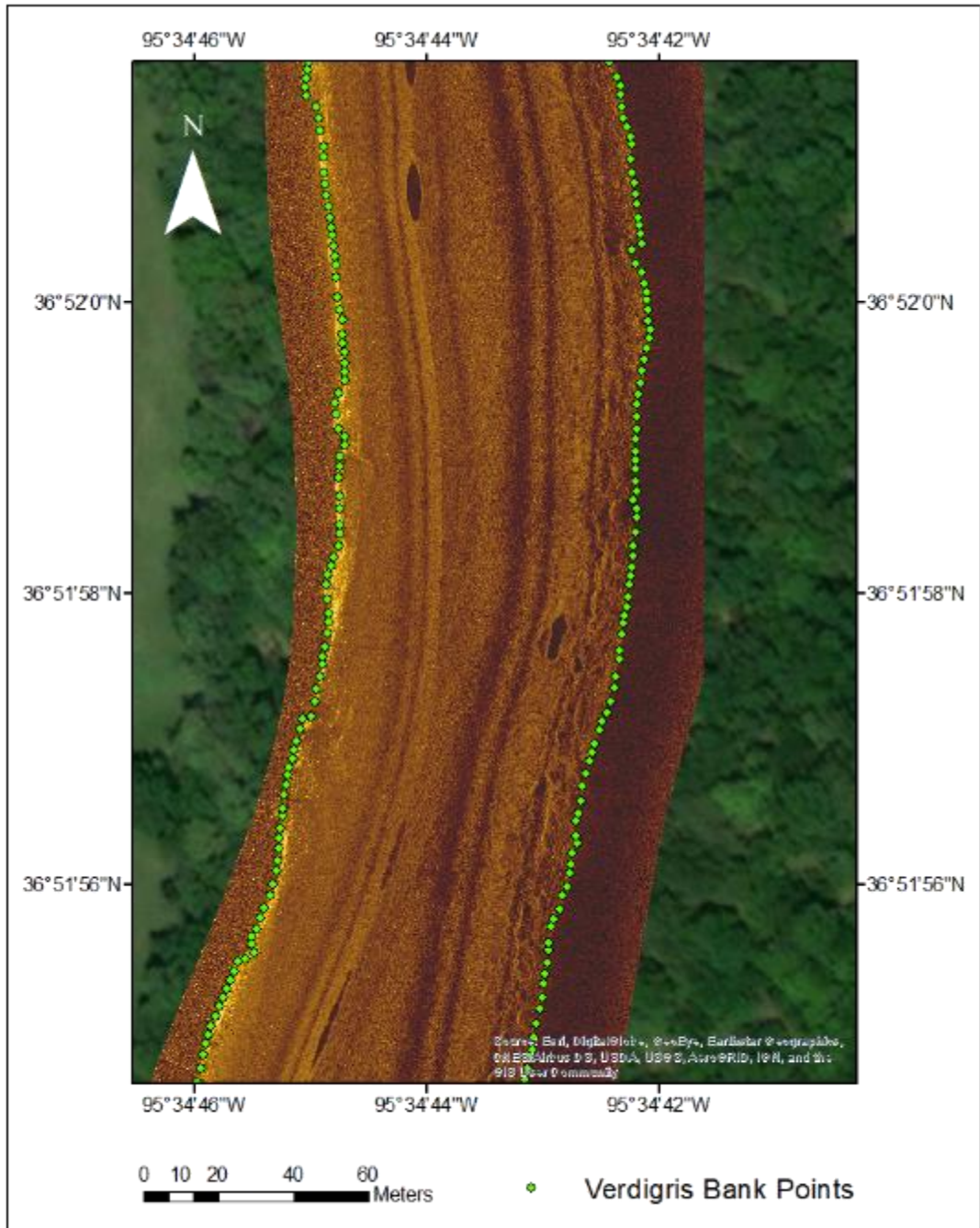


Figure 3. Example from the Verdigris River illustrating how the bank was identified from SSS imagery when bank to bank coverage was available. Points were created in ArcMap 10.5.1 with a minimum distance of 2.5 meters between points.

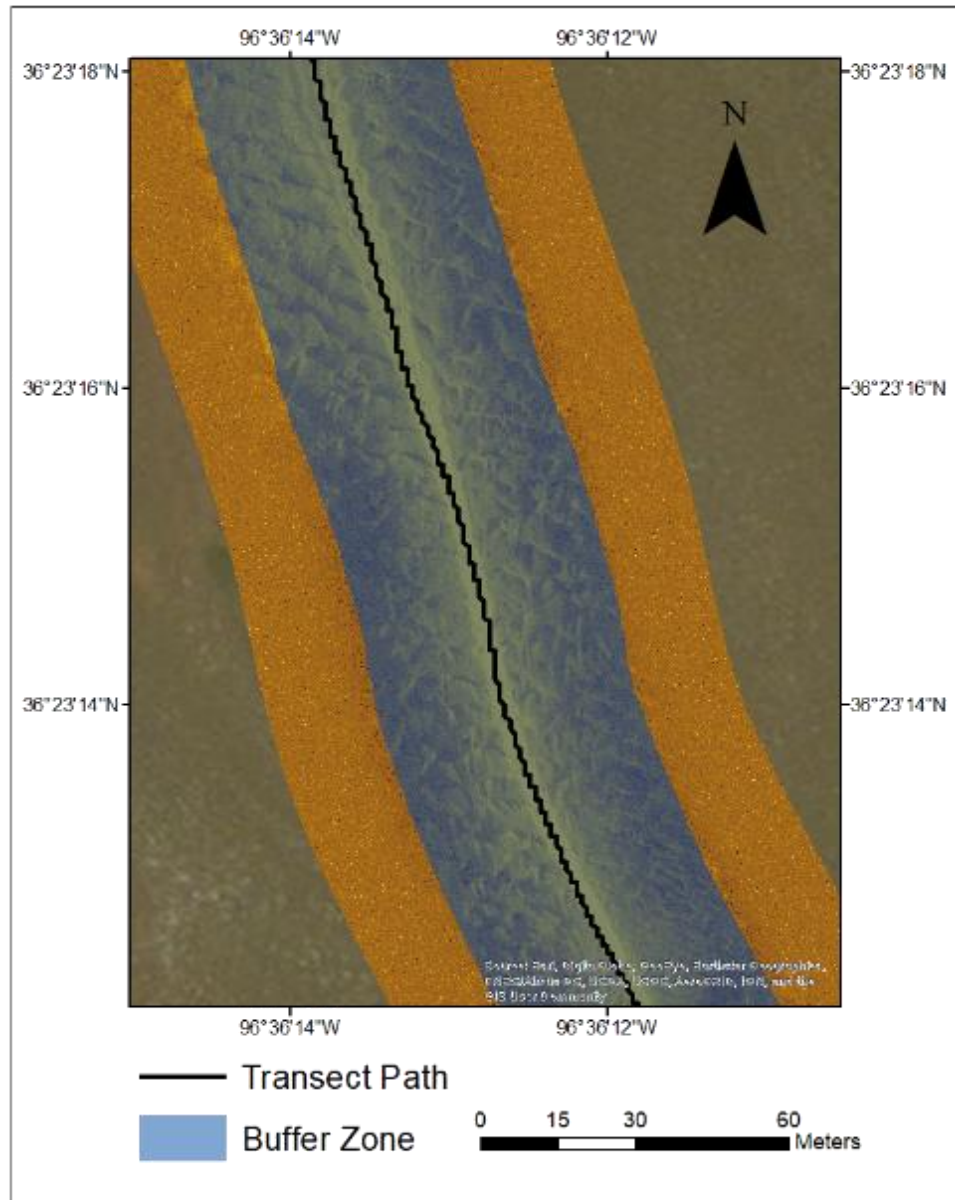


Figure 4. Side-scan sonar imagery collected from the Arkansas River above Keystone Lake overlaid on top of aerial imagery demonstrating the buffer technique applied to imagery. The average of three measurements at the beginning, middle and end of the perpendicular distance from the transect path to the extent of identifiable imagery was used to create a buffer distance. In this transect a 20.2 meter buffer was applied to each side of the imagery to identify the area surveyed.

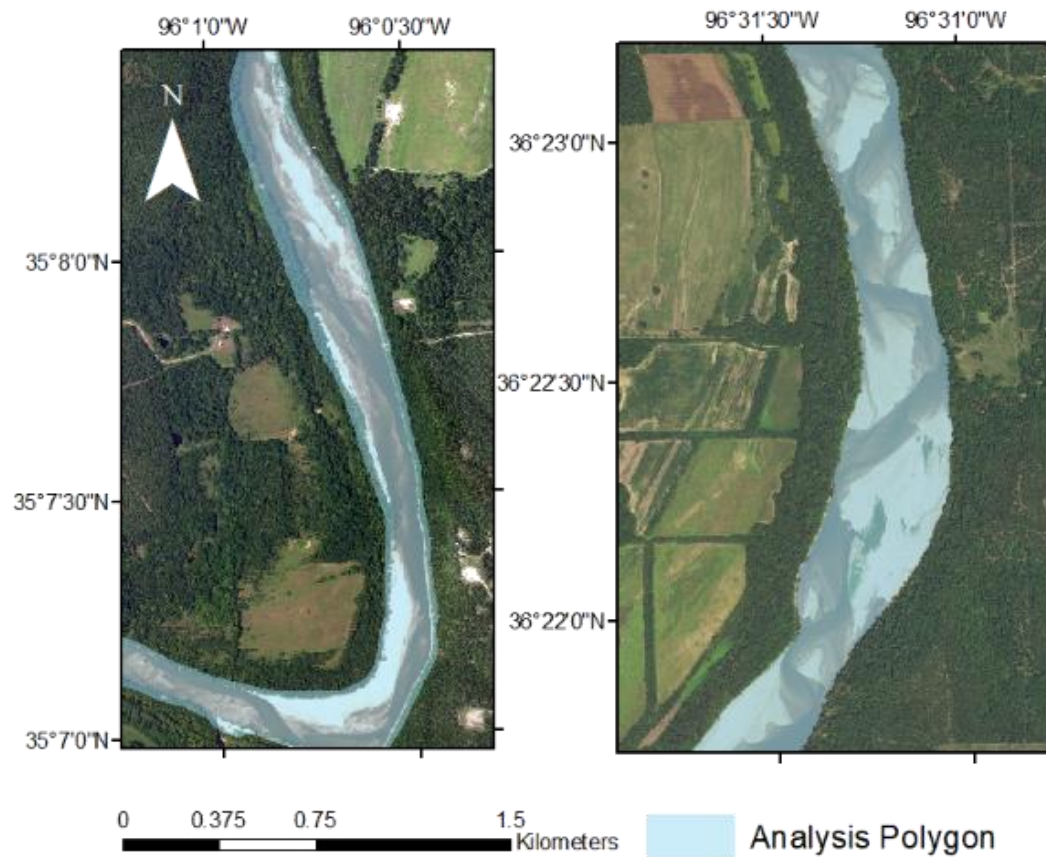


Figure 5. An example of polygons created for supervised classification of aerial imagery using the maximum likelihood classification method. Left image displays a manually drawn polygon on 2015 NAIP imagery of the Canadian River during flows at the 25th percentile of mean annual discharge. The right displays an analysis polygon created from supervised classification of high flow imagery from 2013 during flows of the 96th percentile overlaid onto 2017 NAIP imagery of Arkansas River above Keystone Lake during flows at the 22nd percentile of mean annual discharge.

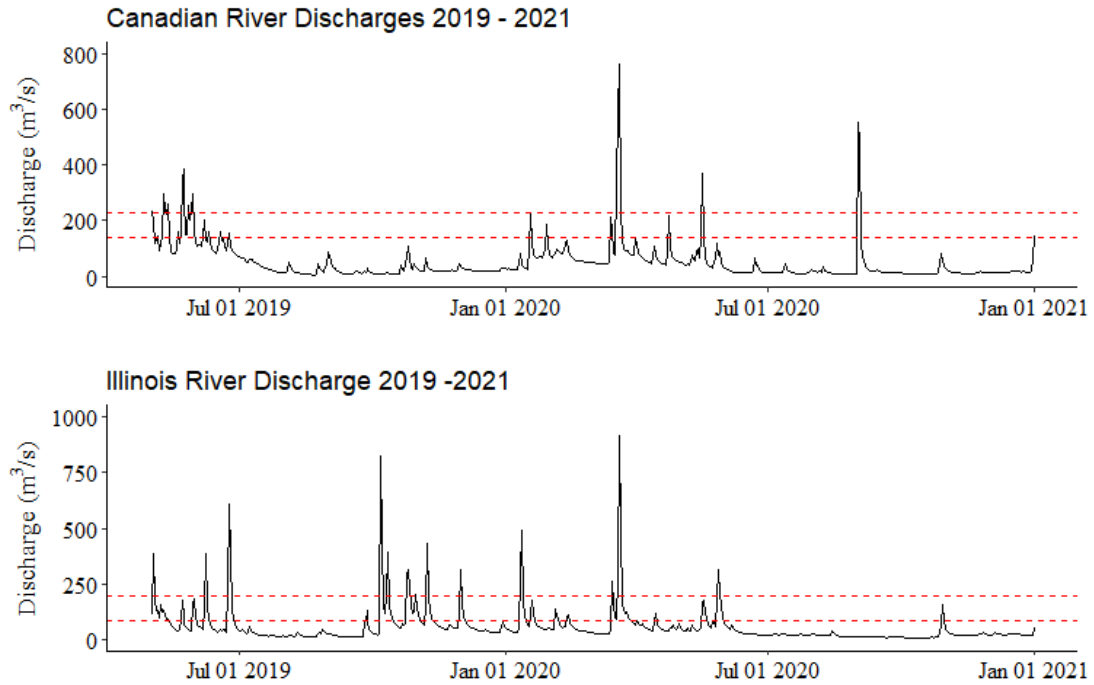


Figure 6. Hydrographs from the Canadian River (Top) and Illinois River (Bottom), red dashed lines indicate the minimum discharge necessary to survey the river from in person experience and the maximum threshold for sampling based on safety of the survey crew. Average sampling window for each river was calculated by average consecutive days with discharge between maximum and minimum necessary flows.

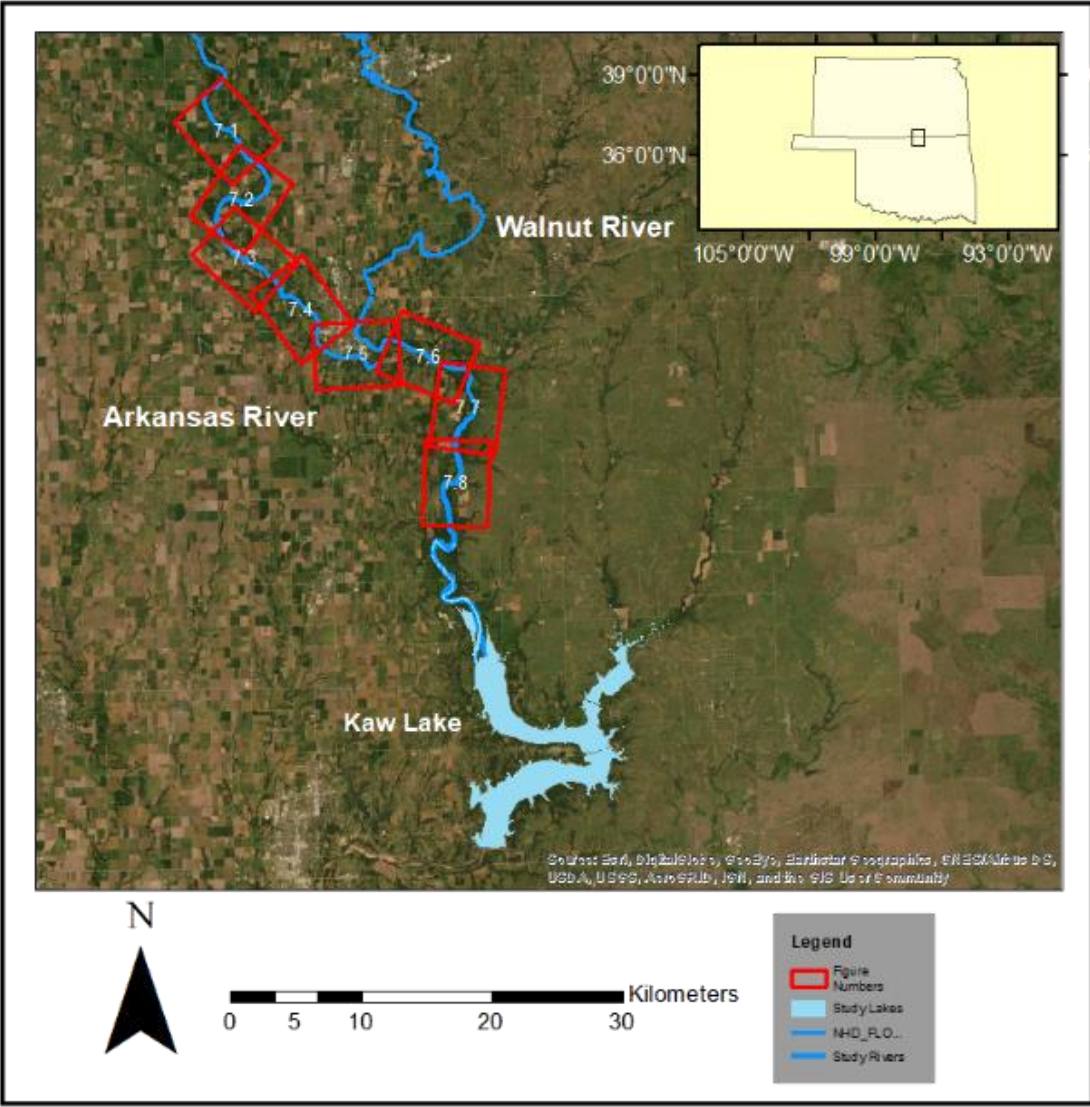


Figure 7. Study area for the Arkansas and Walnut rivers as a part of the Kaw Lake system, overlaid onto USDA aerial imagery in north central Oklahoma and south central Kansas. Higher resolution substrate maps of the Arkansas and Cimarron rivers are depicted in Figures 7.1-7.8, as indicated in red boxes. Figure 7.5 contains extents of the Arkansas River as well as the full extent of Walnut River mapping.

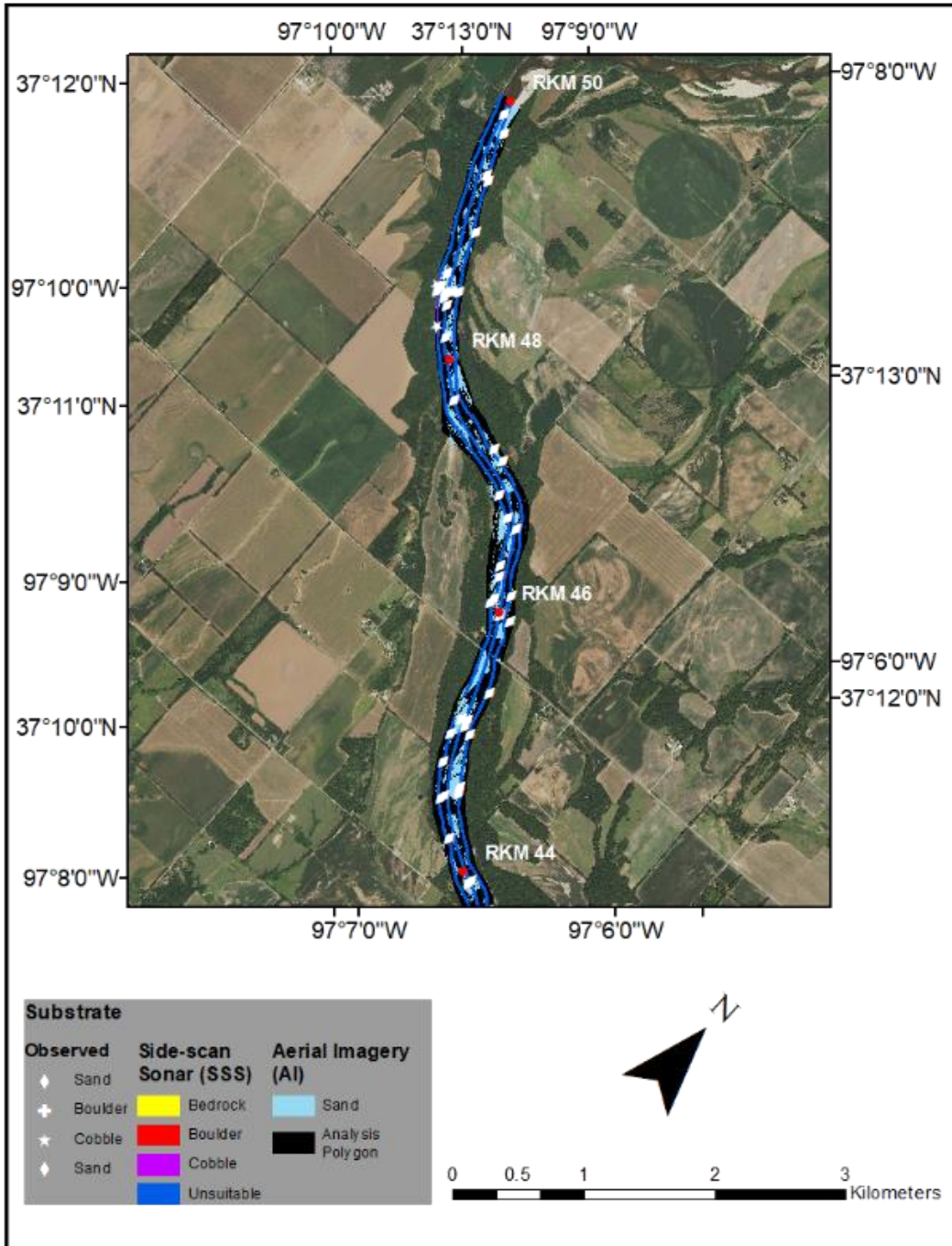


Figure 7.1

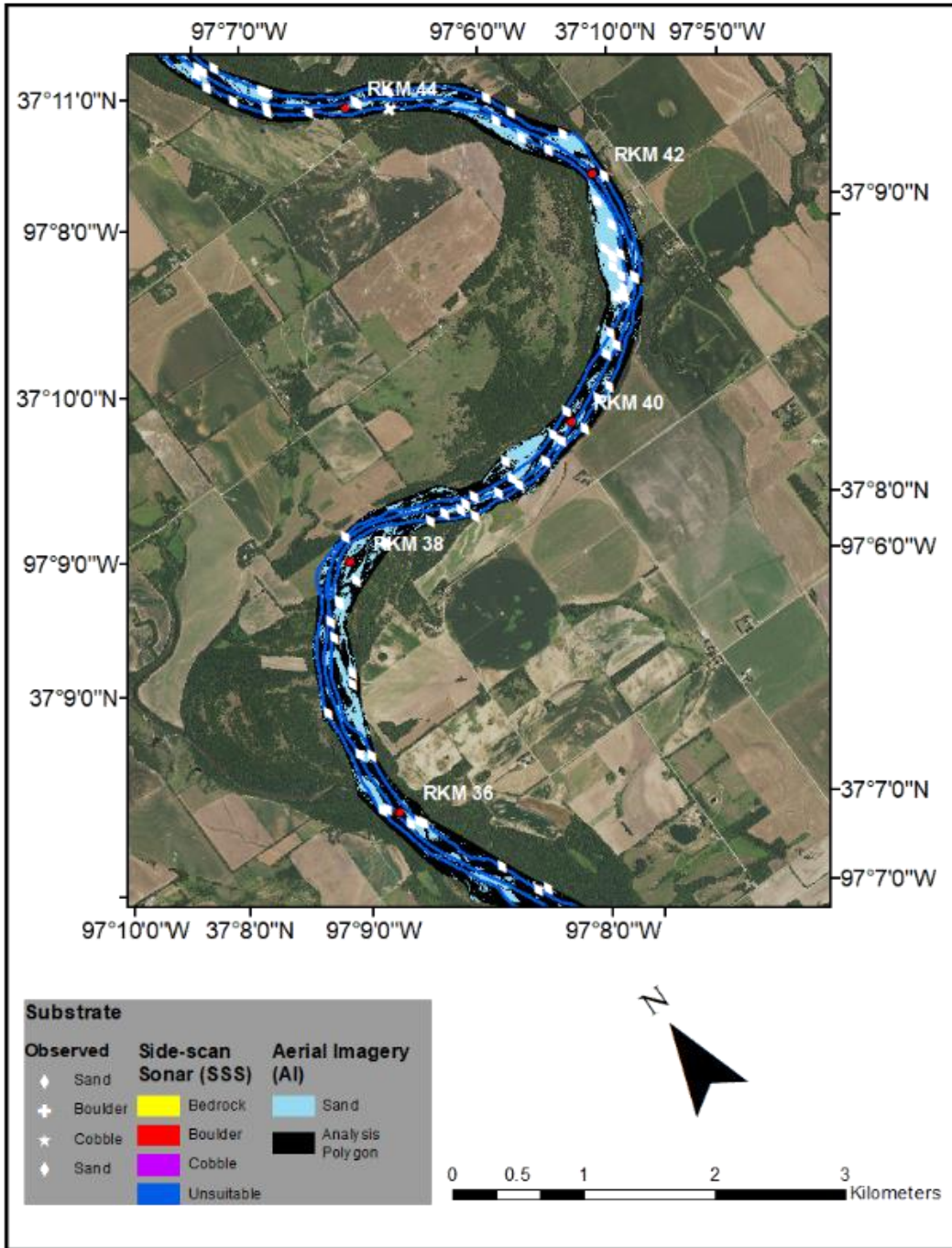


Figure 7.2

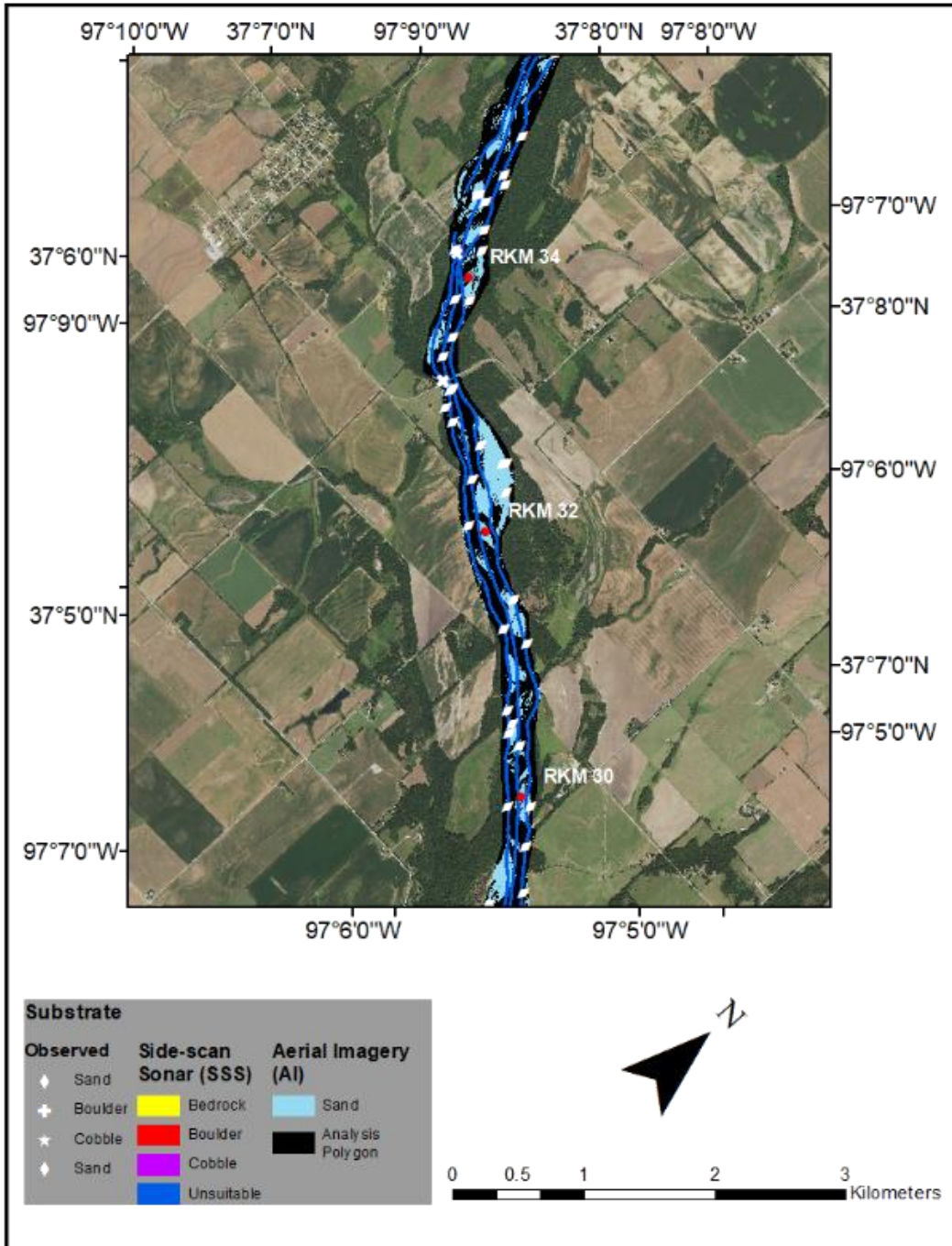


Figure 7.4

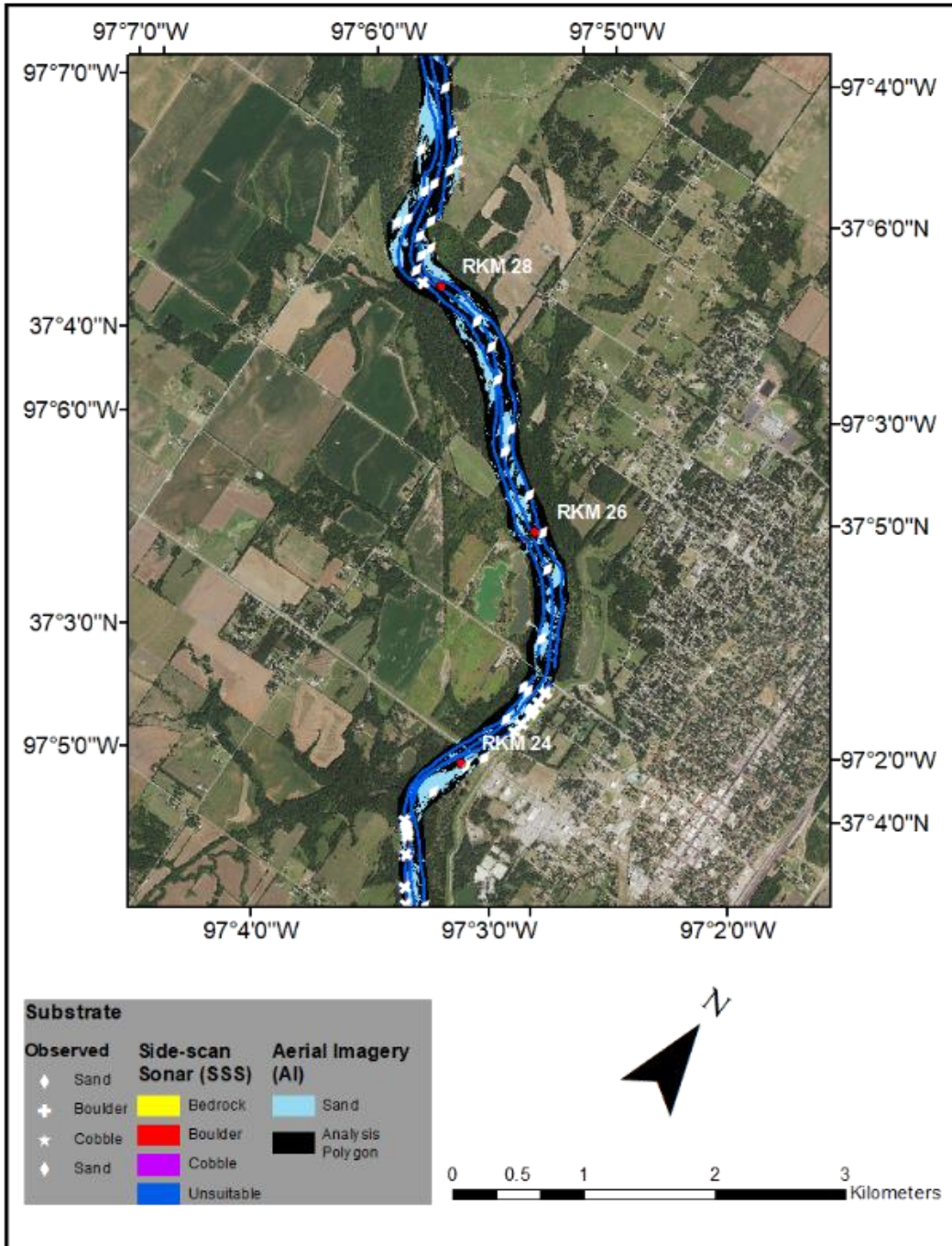


Figure 7.5

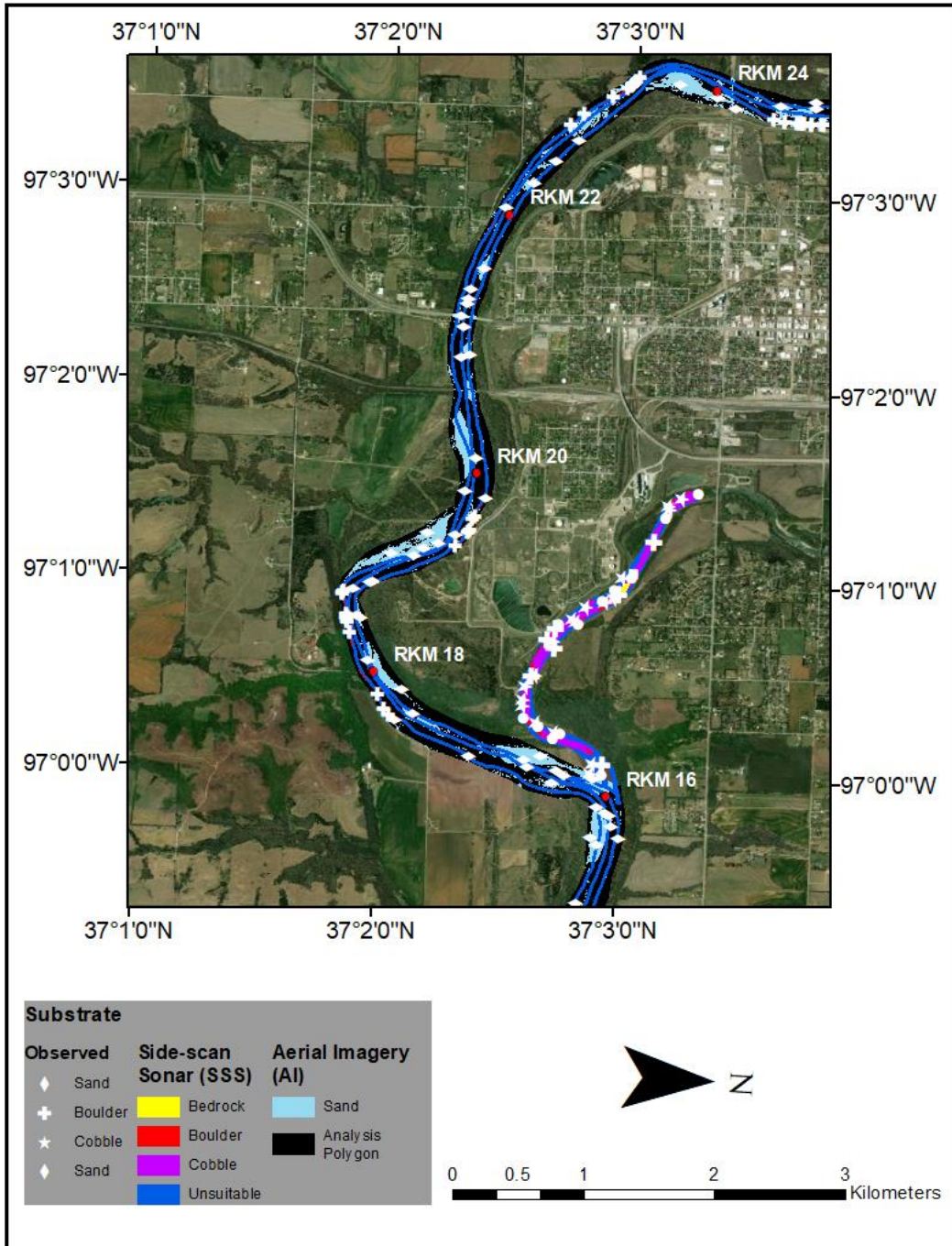


Figure 7.6

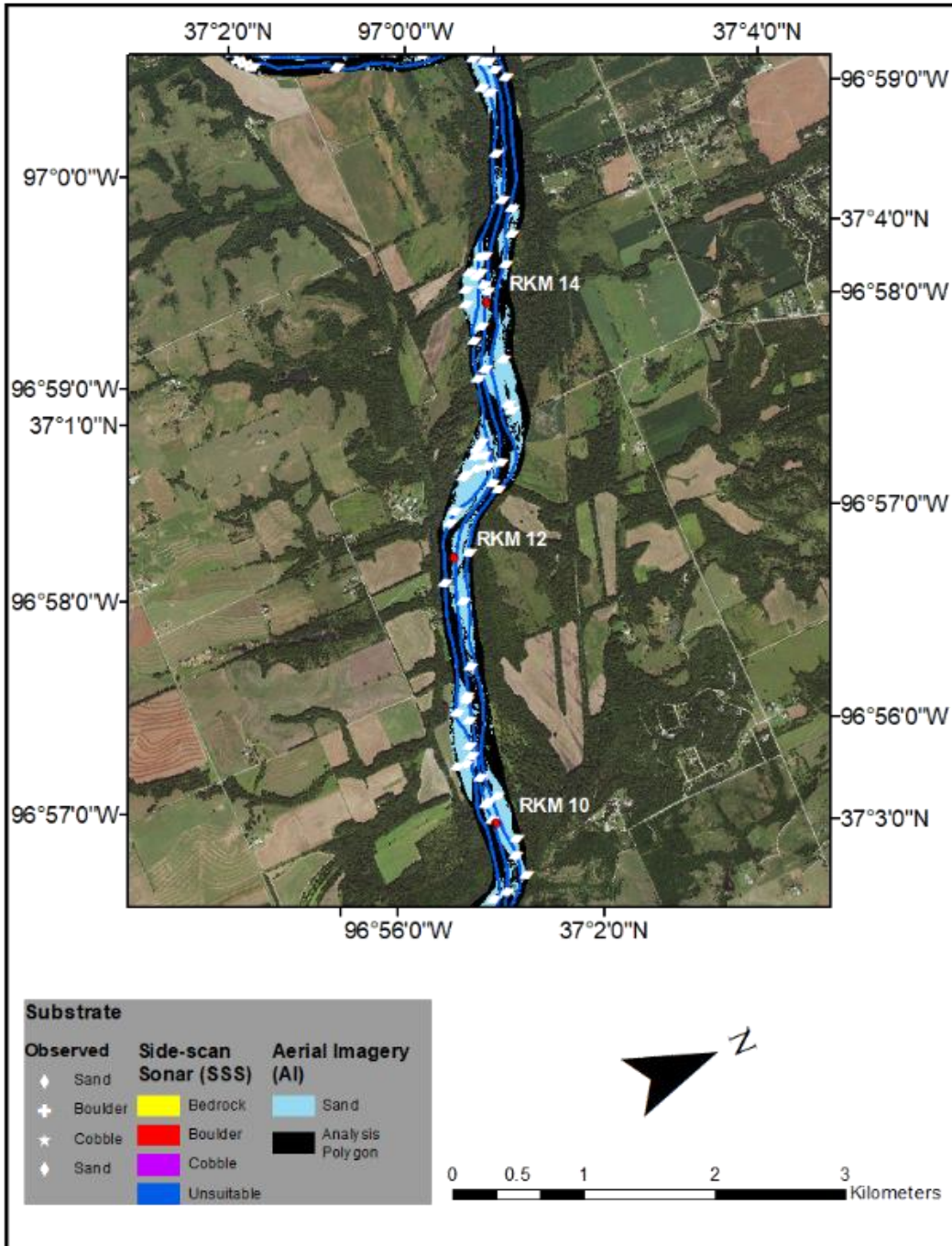


Figure 7.7

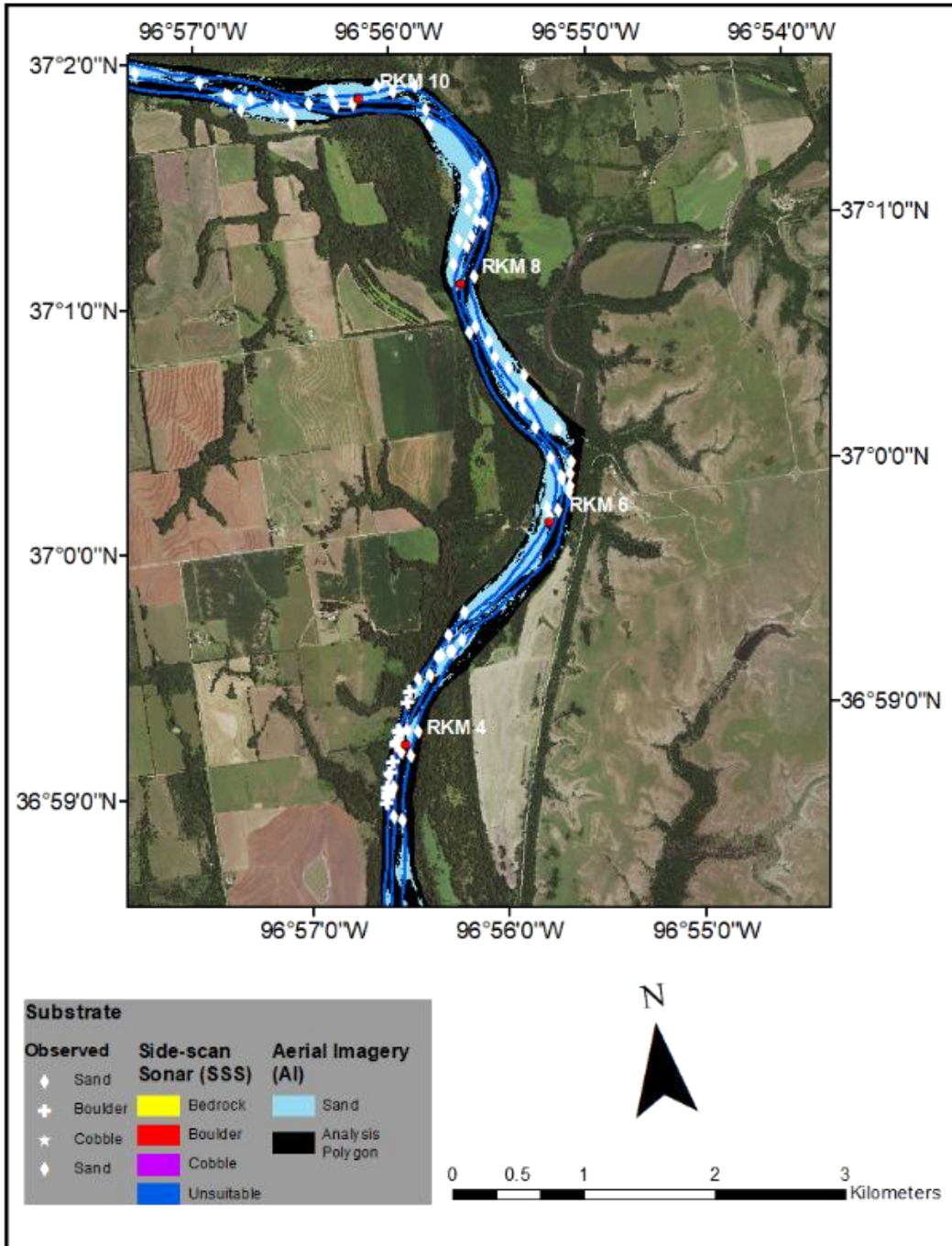


Figure 7.8

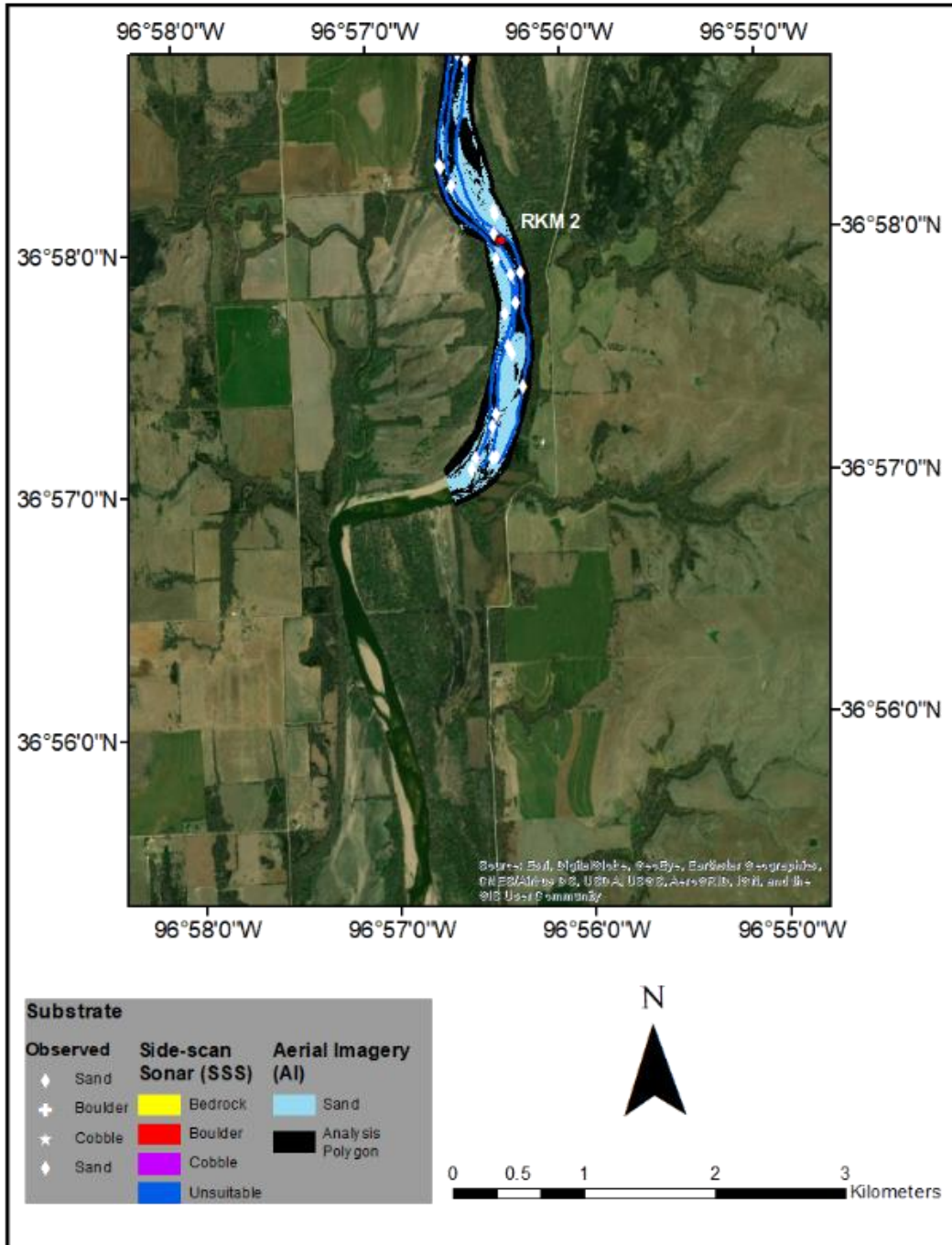


Figure 7.10

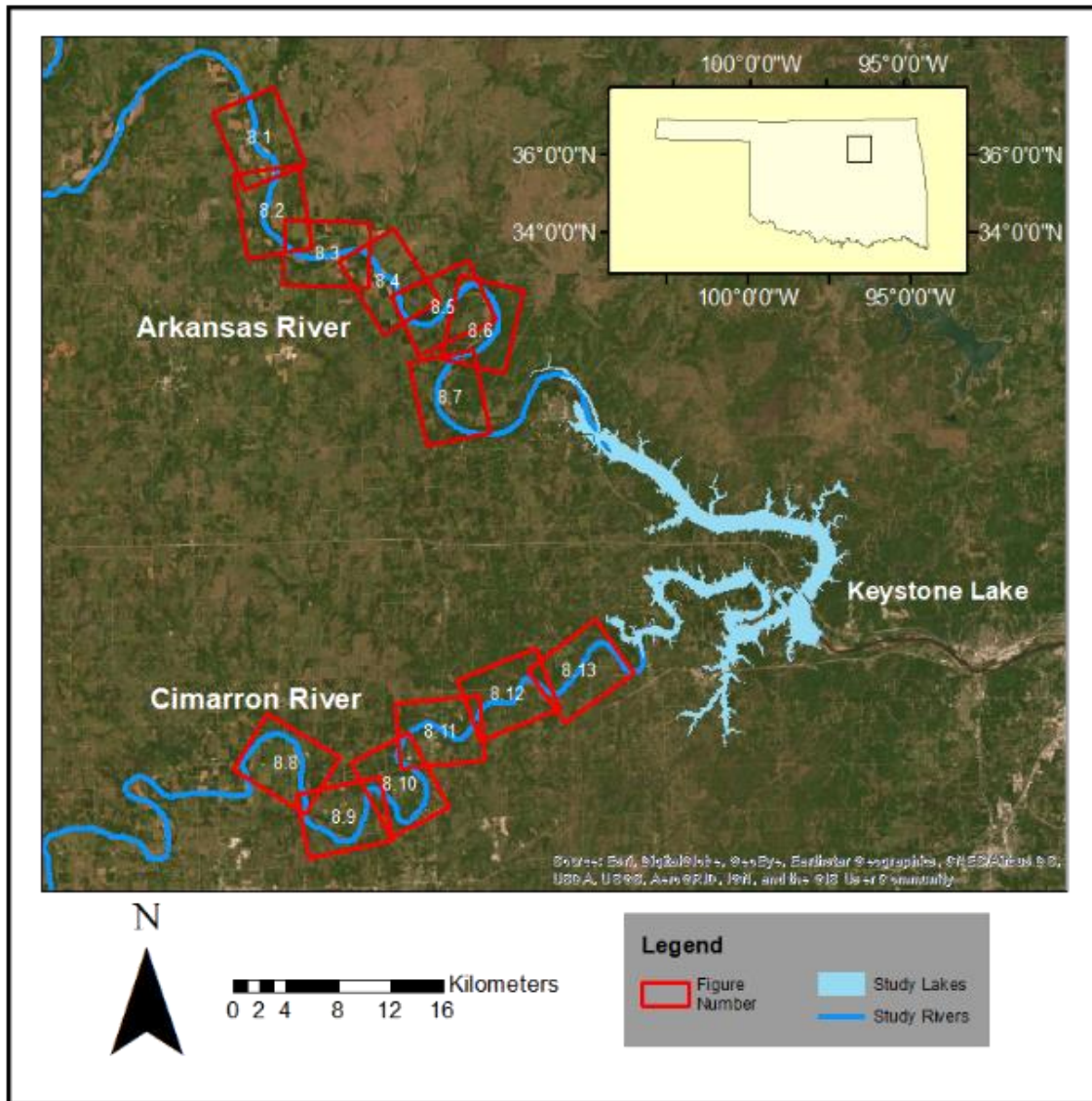


Figure 8. Study area for the Arkansas and Cimarron rivers as a part of the Keystone Lake system, overlaid onto USDA aerial imagery in north central Oklahoma. Higher resolution substrate maps of the Arkansas and Cimarron rivers are depicted in Figures 8.1-8.13, as indicated in red boxes.

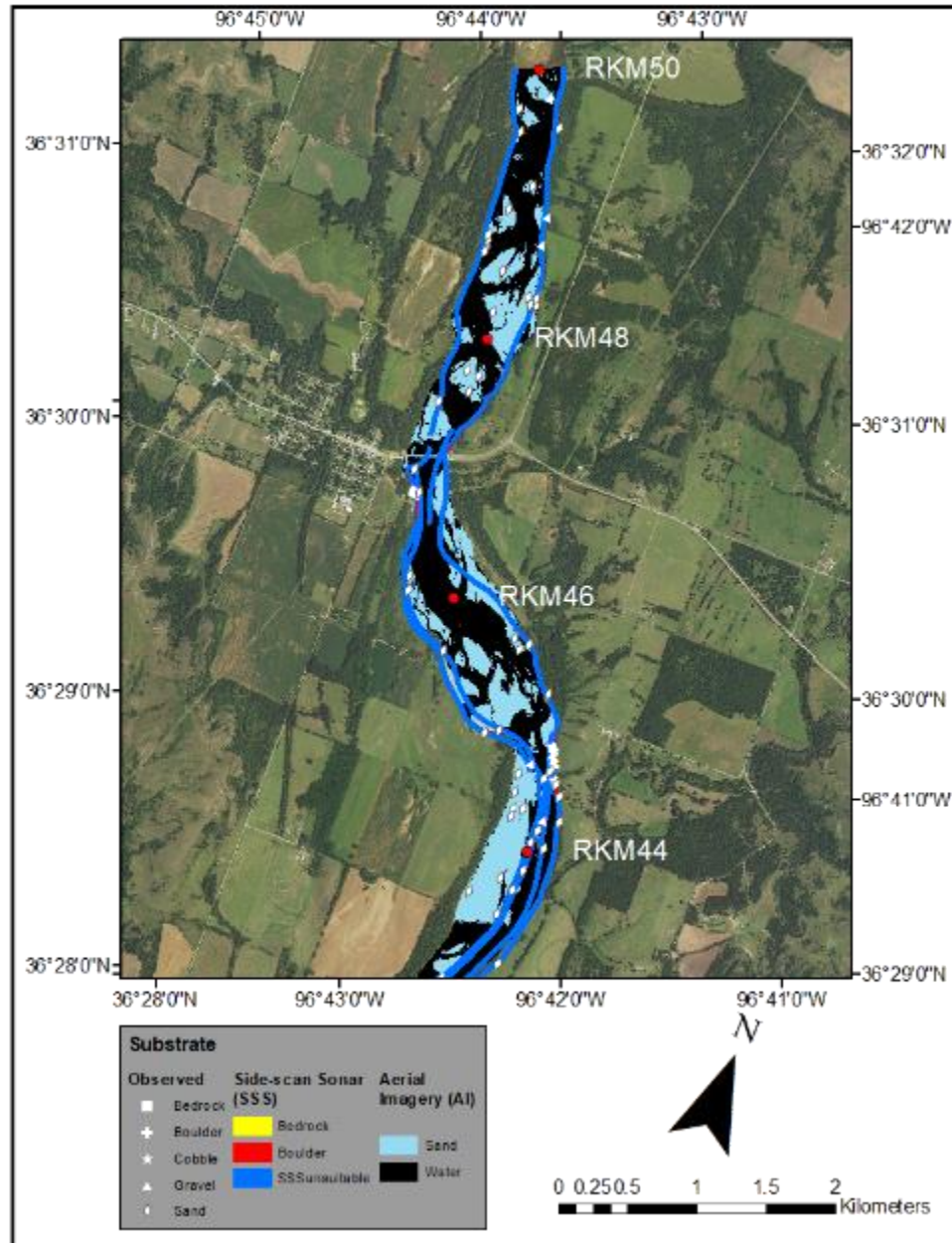


Figure 8.1 Substrate classification maps for the Arkansas River above Keystone Lake overlaid on 2013 NAIP imagery (National Agriculture Imagery Program). Substrate classifications are grouped according to their method (Aerial imagery (AI) and side-scan sonar (SSS)). Symbols are given for ground truthing points according to the substrate that was found to be present at said point. Maps are listed from upstream to downstream according to river kilometers from the river-reservoir interface of Keystone Lake.

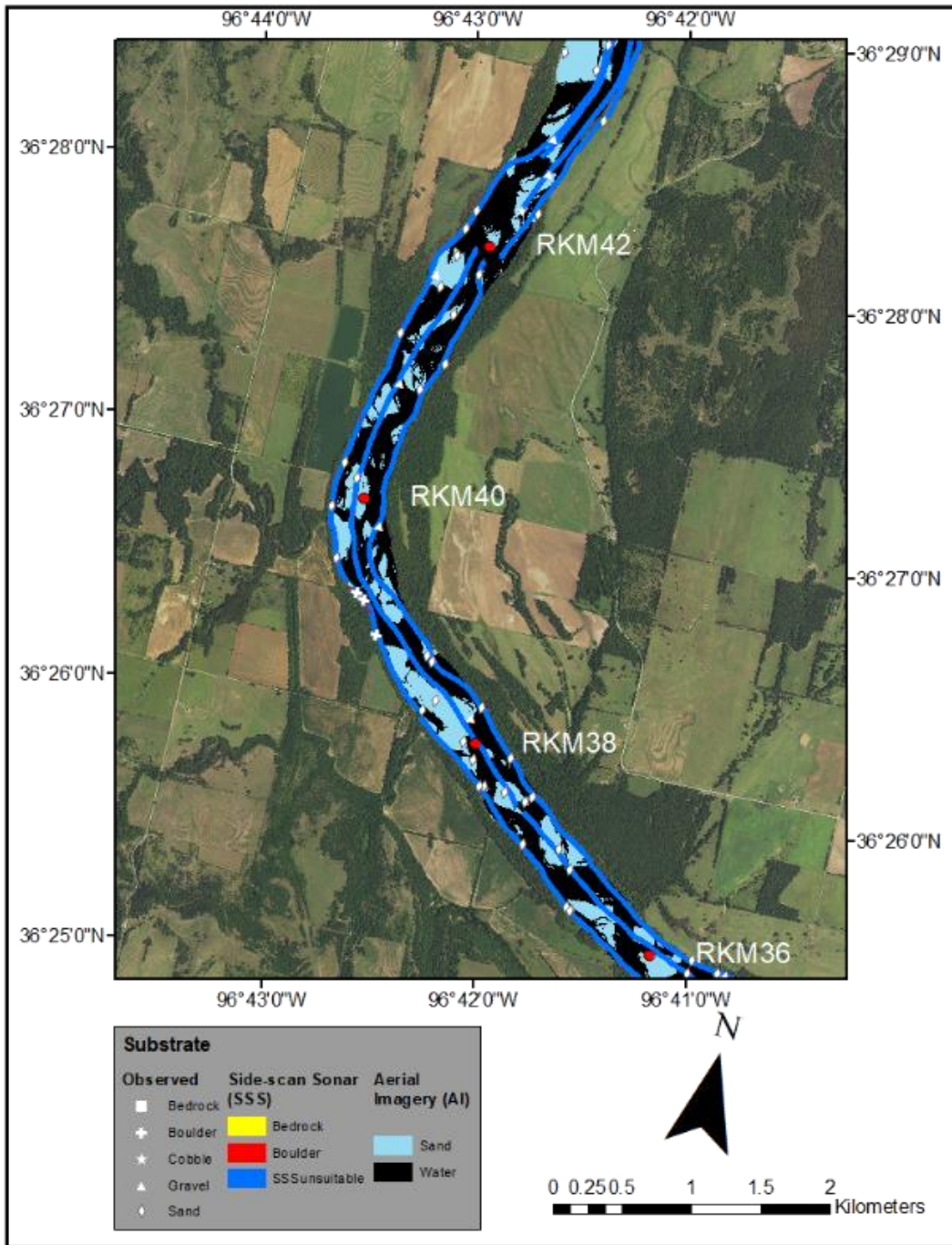


Figure 8.2

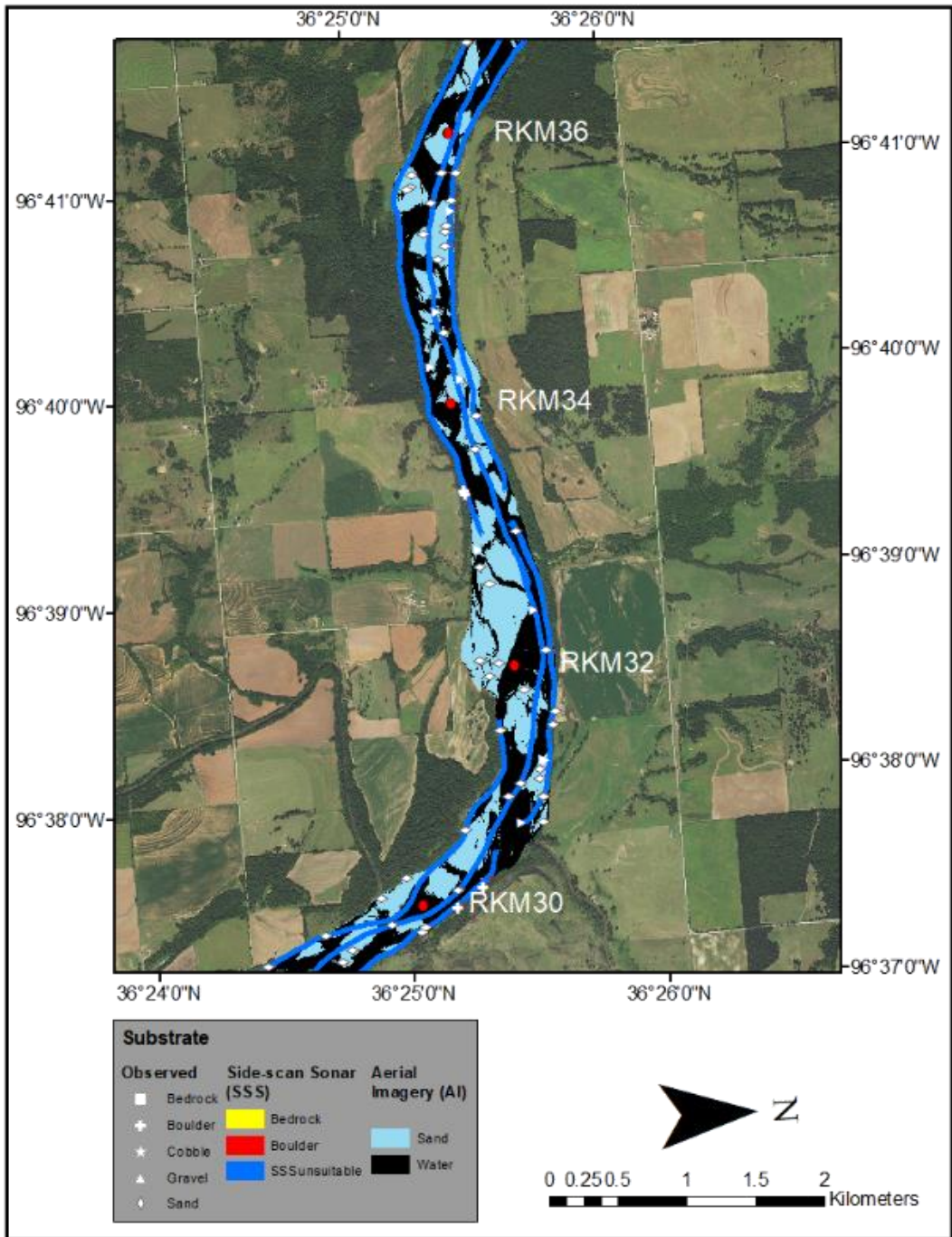


Figure 8.3

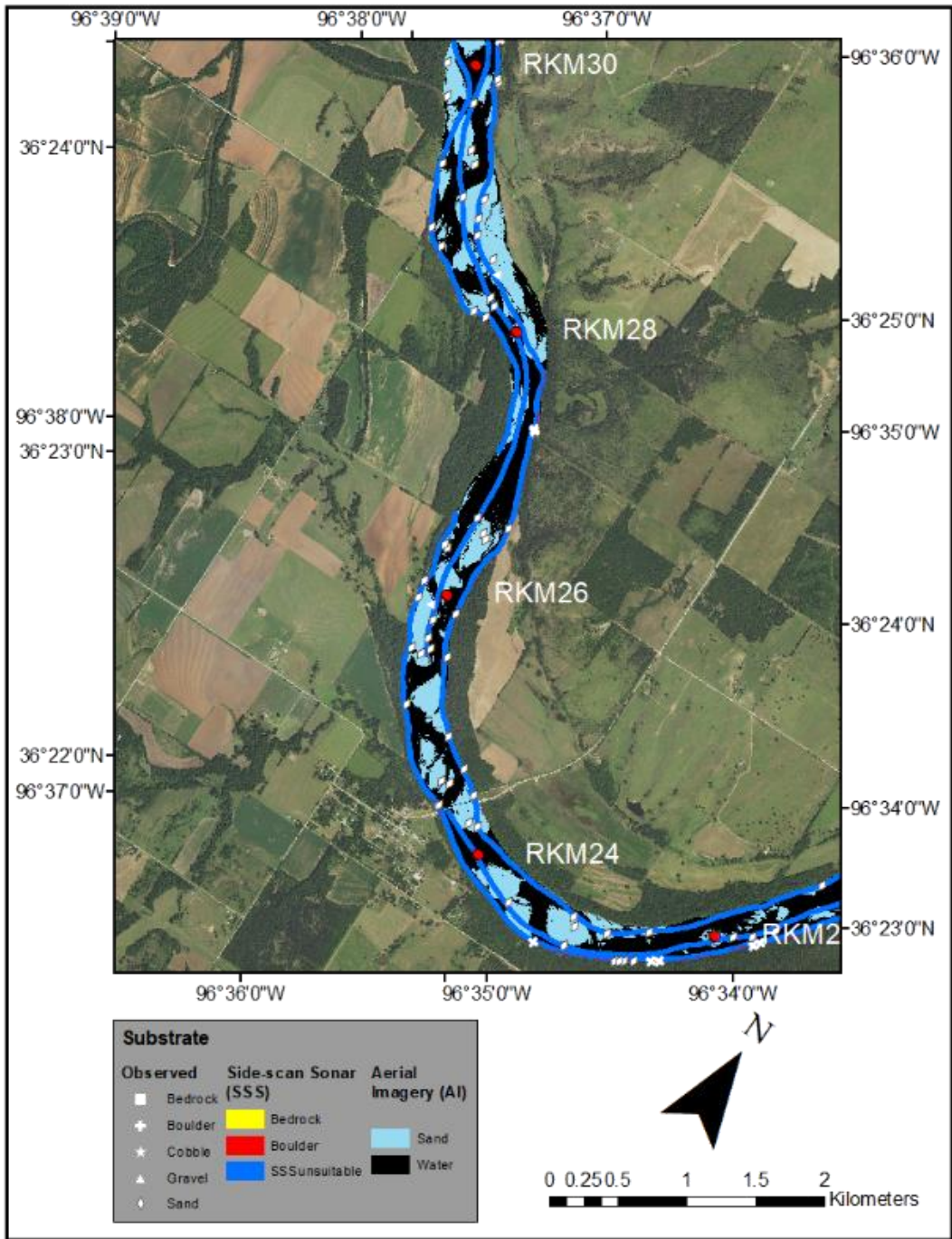


Figure 8.4

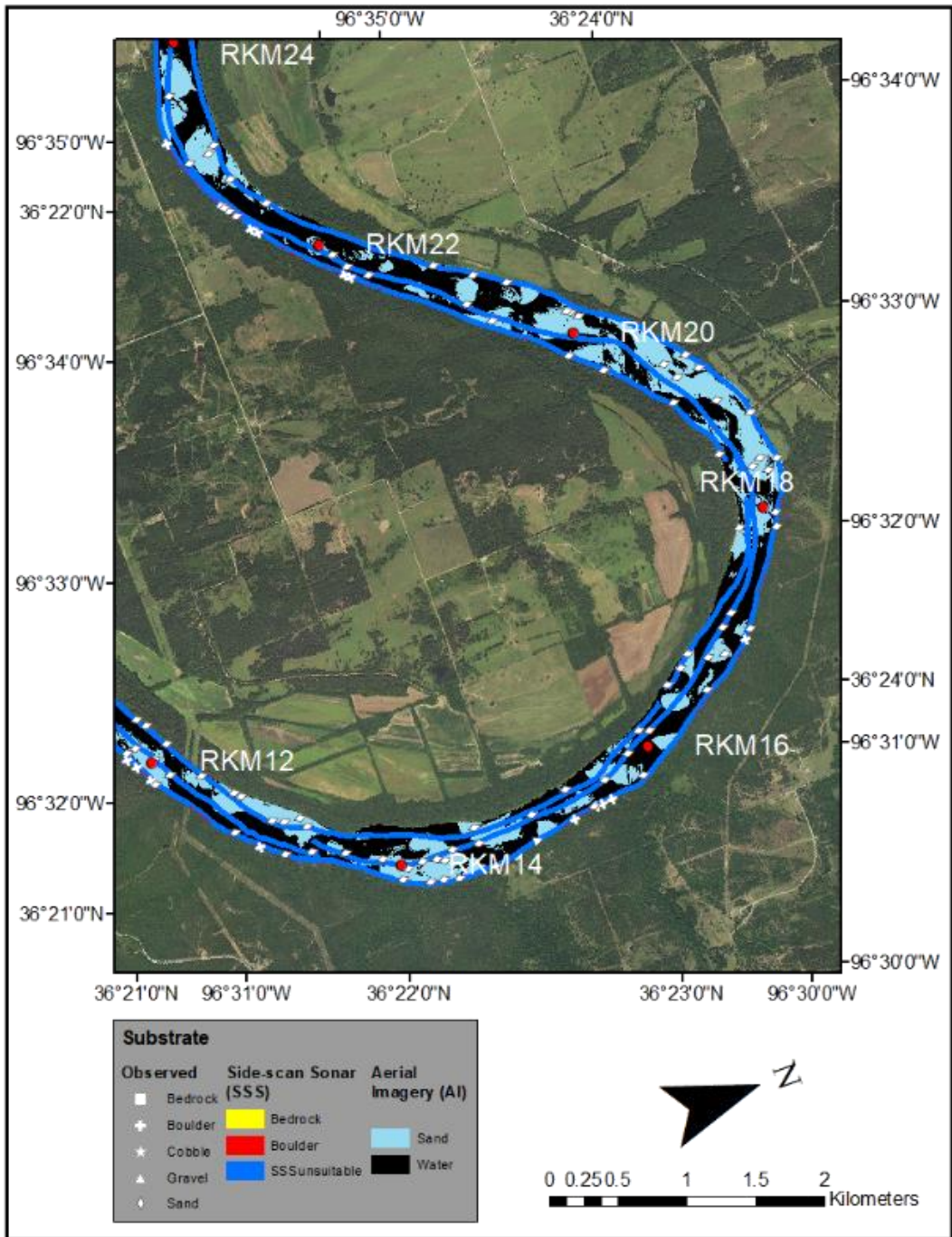


Figure 8.5

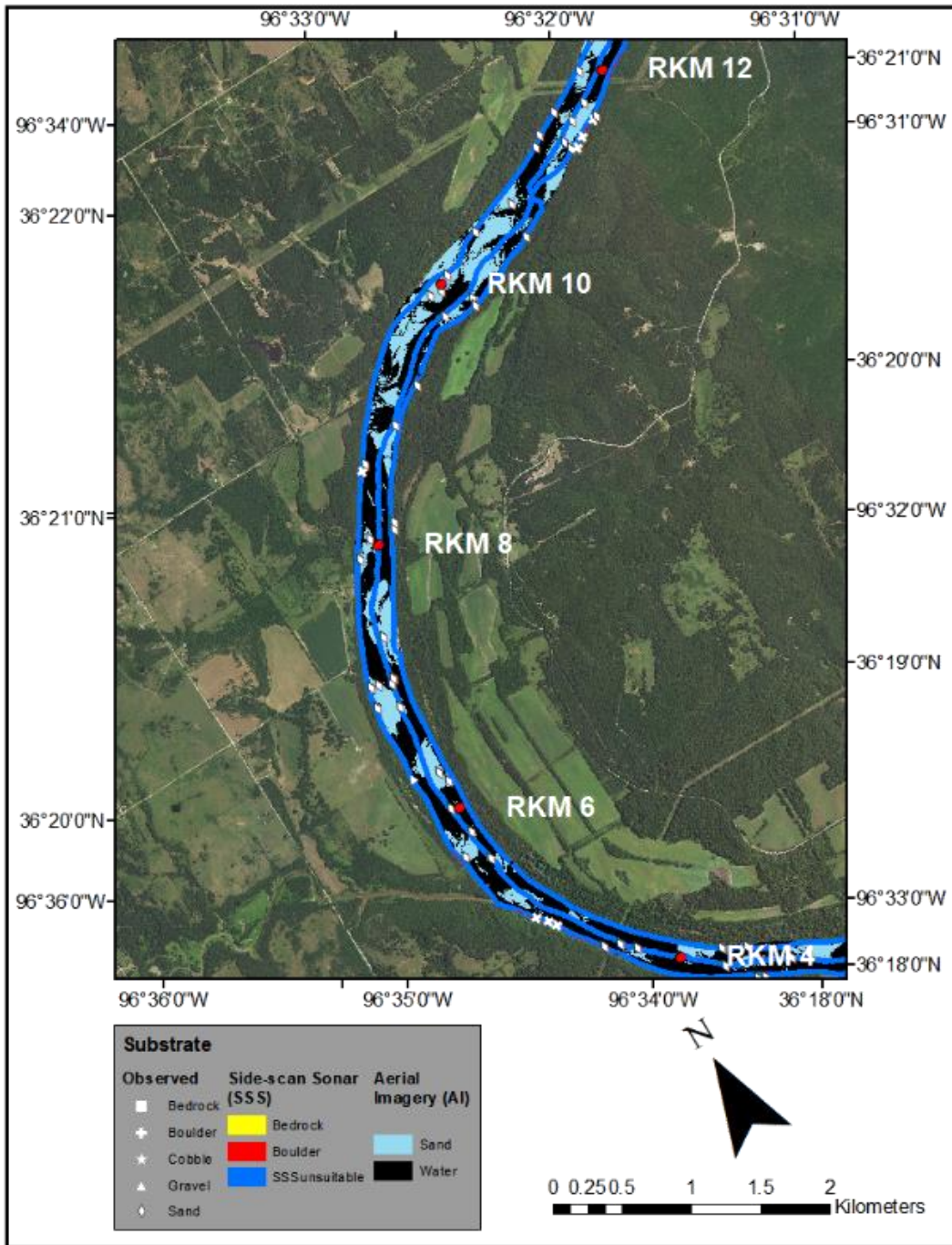


Figure 8.6

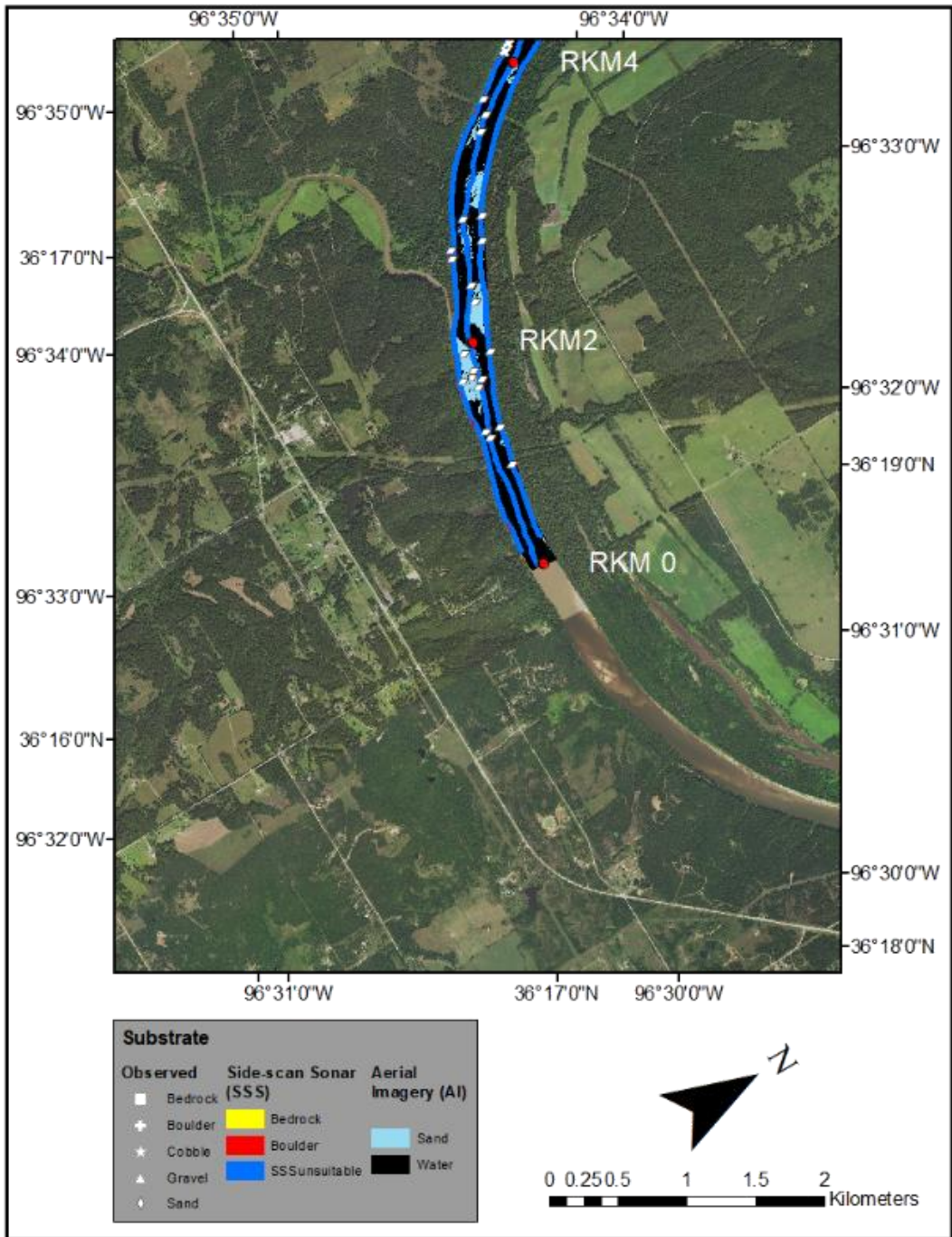


Figure 8.7

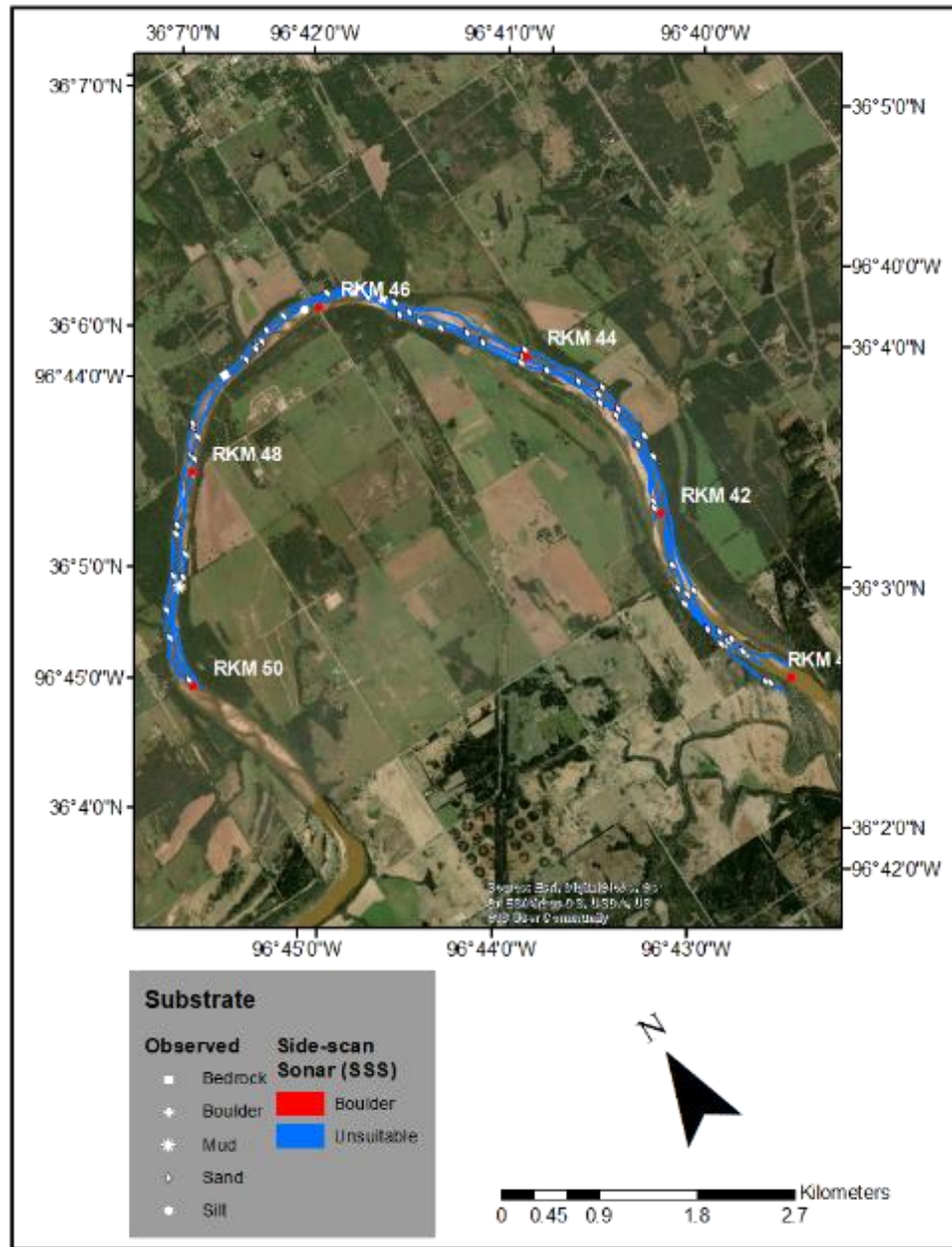


Figure 8.8 Substrate classification maps for the Cimarron River overlaid on USDA aerial imagery. Substrate classifications are classified by unsuitable or type of suitable substrate as determined by side-scan sonar. Symbols are given for ground truthing points according to the substrate that was found to be present at said point. Maps are listed from upstream to downstream according to river kilometers from the river-reservoir interface of Keystone Lake.

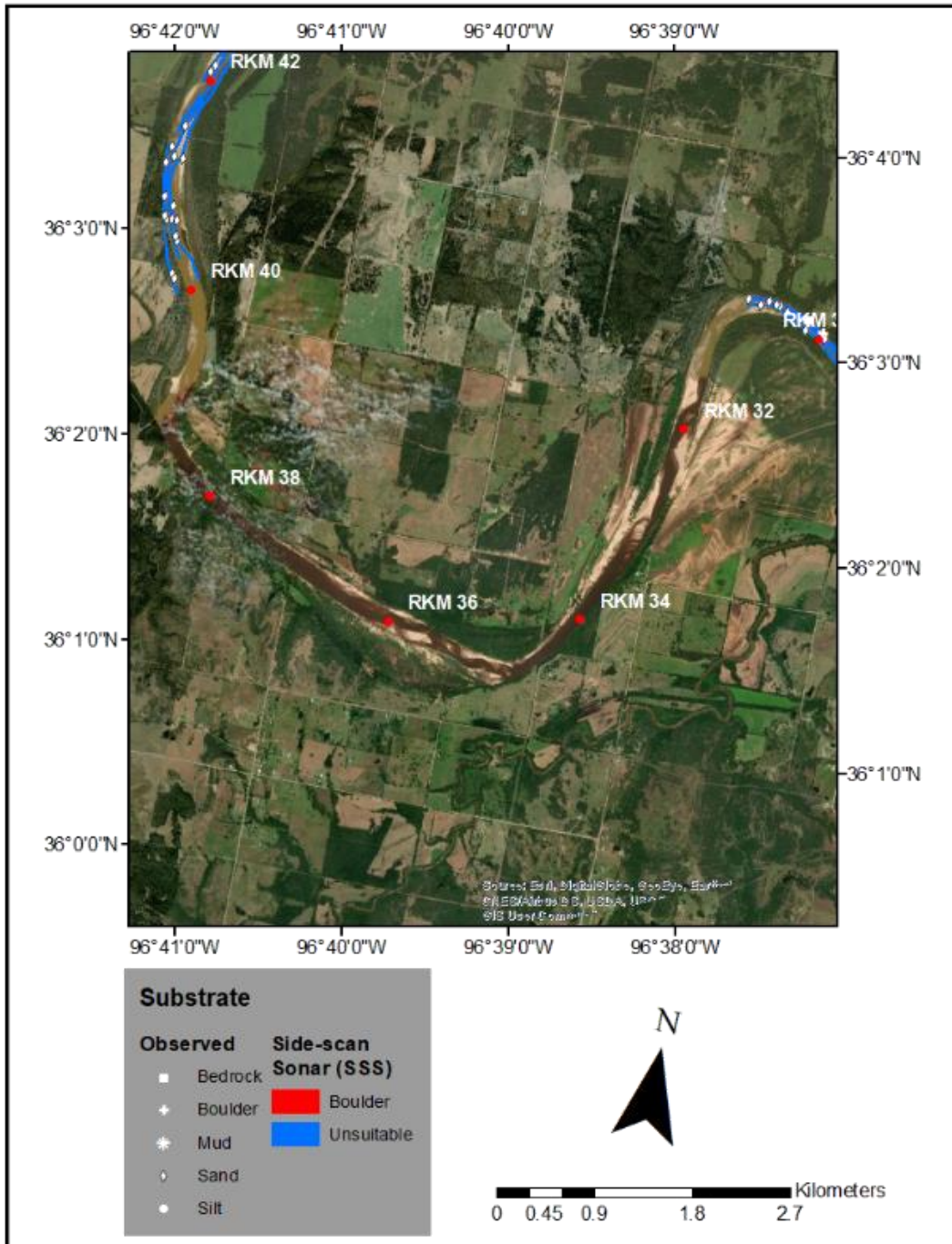


Figure 8.9

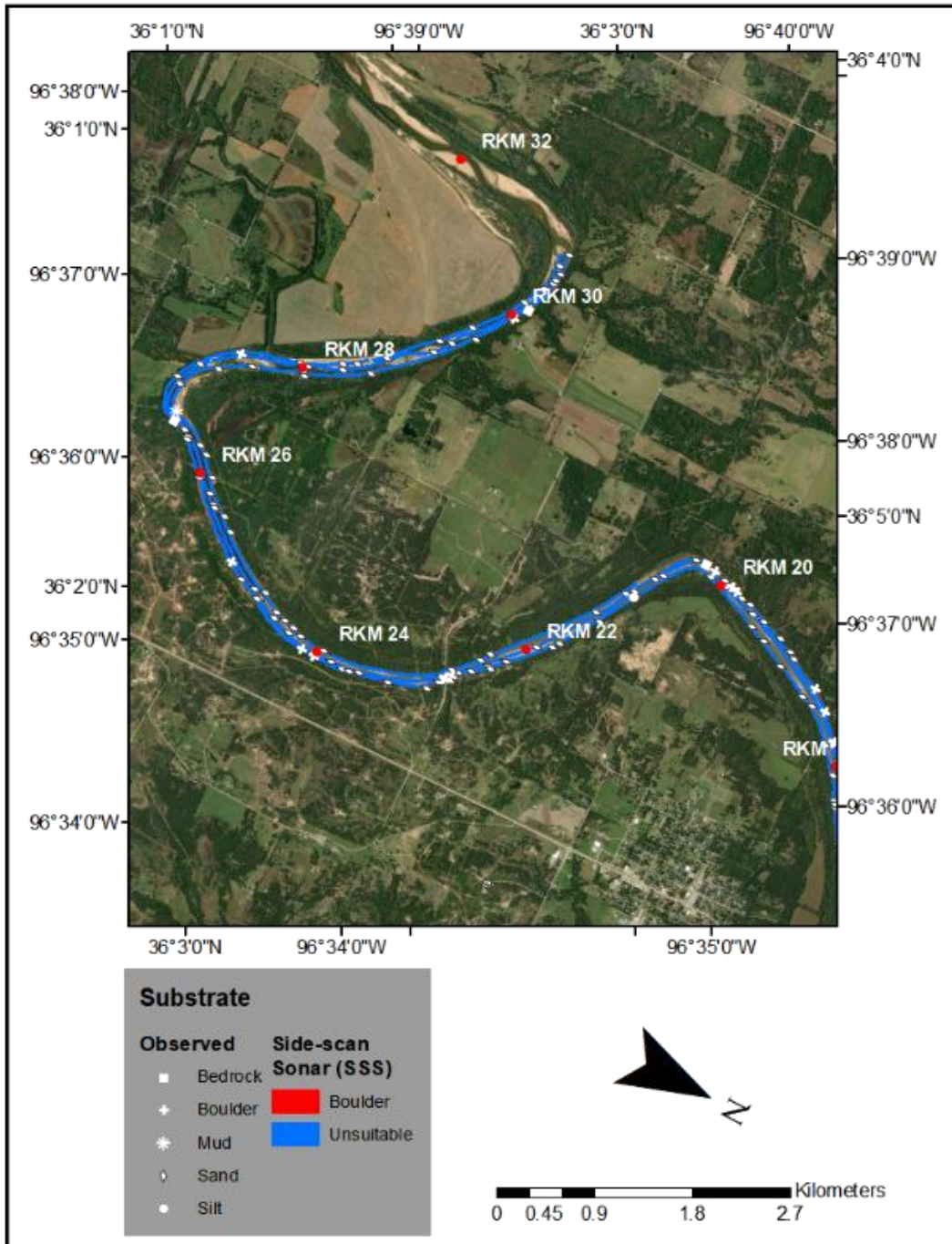


Figure 8.10

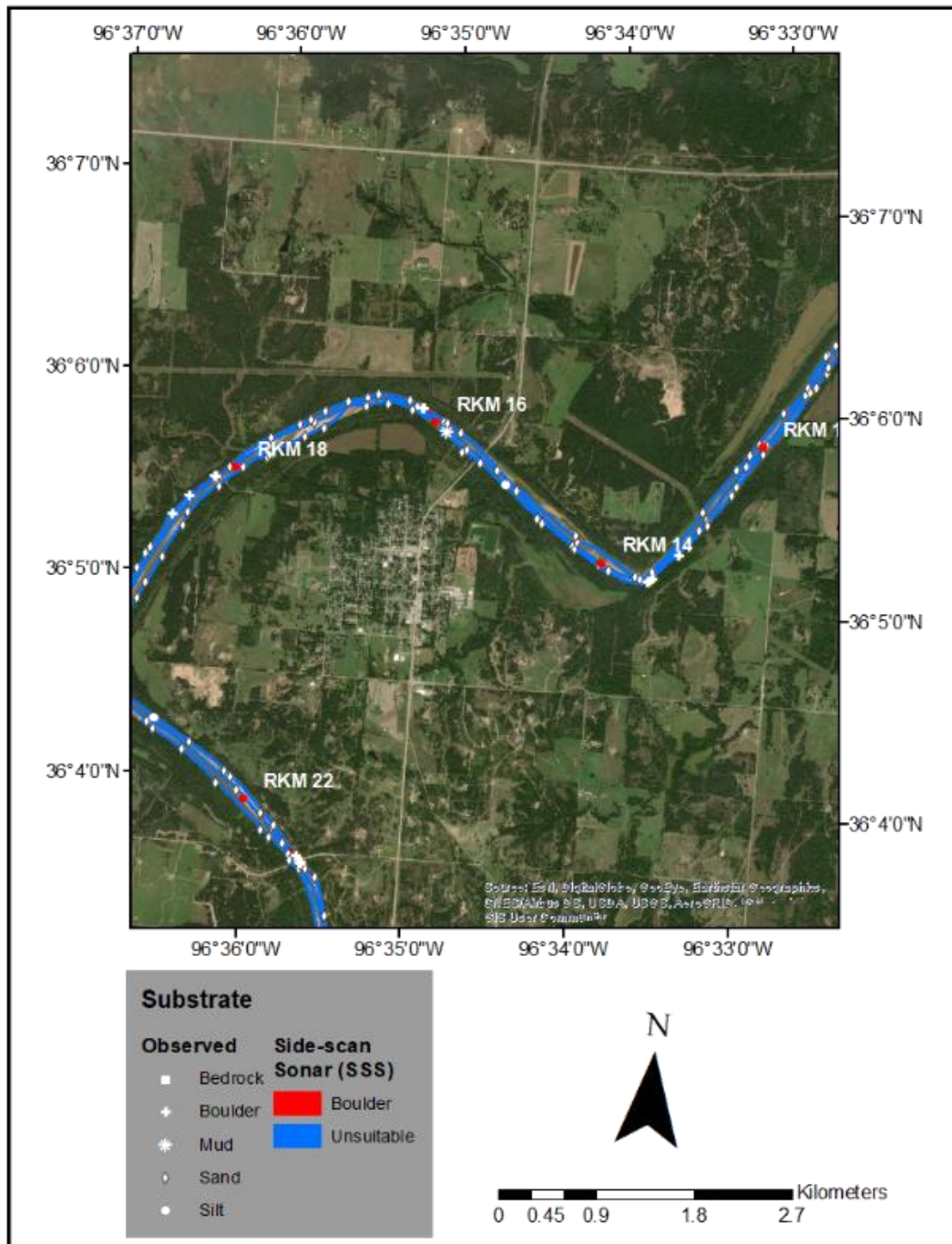


Figure 8.11

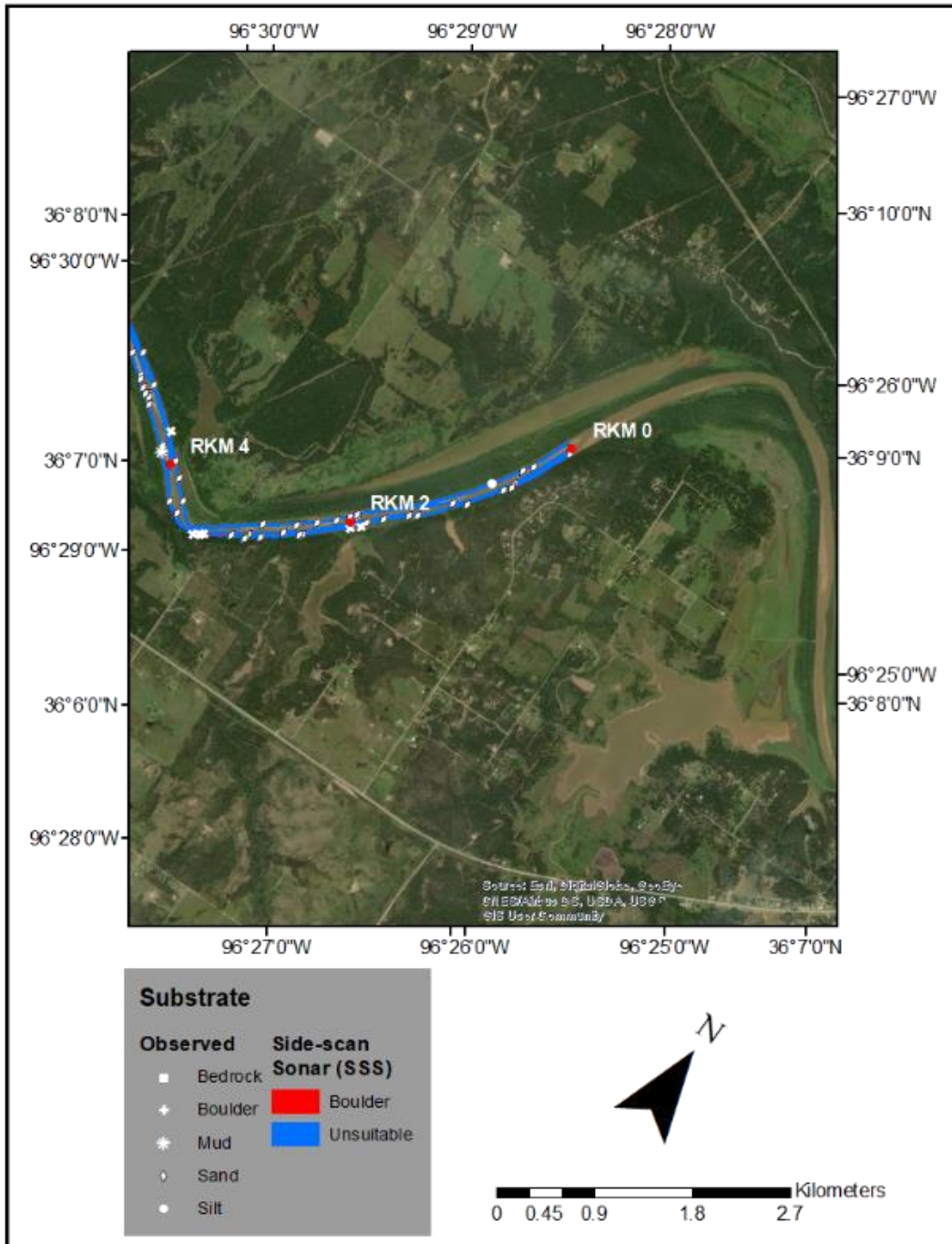


Figure 8.13

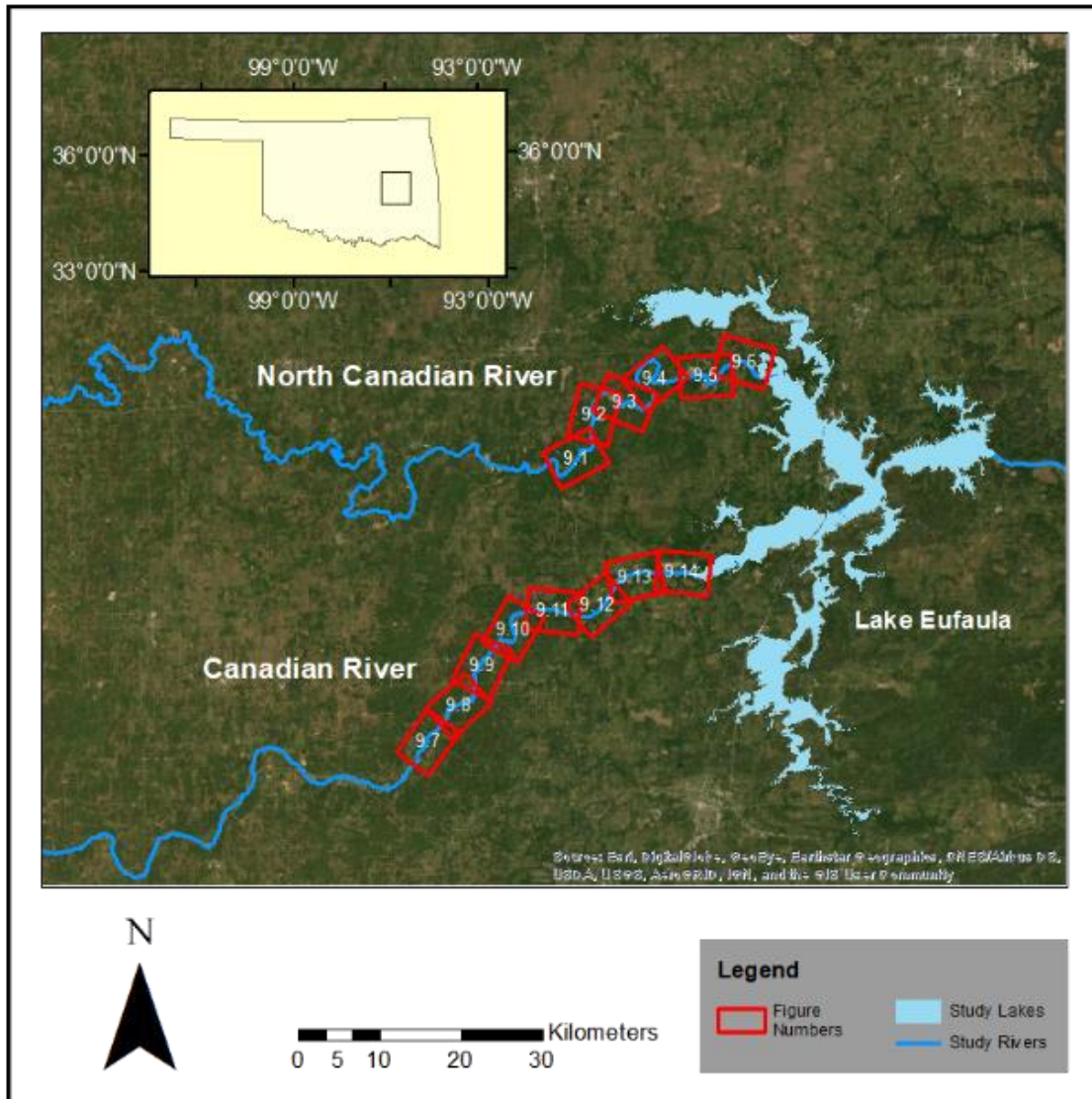


Figure 9. Study area for the North Canadian and Canadian rivers as a part of the Lake Eufaula system, overlaid onto USDA aerial imagery in eastern Oklahoma. Higher resolution substrate maps of the North Canadian and Canadian rivers are depicted in Figures 9.1-9.14, as indicated in red boxes.

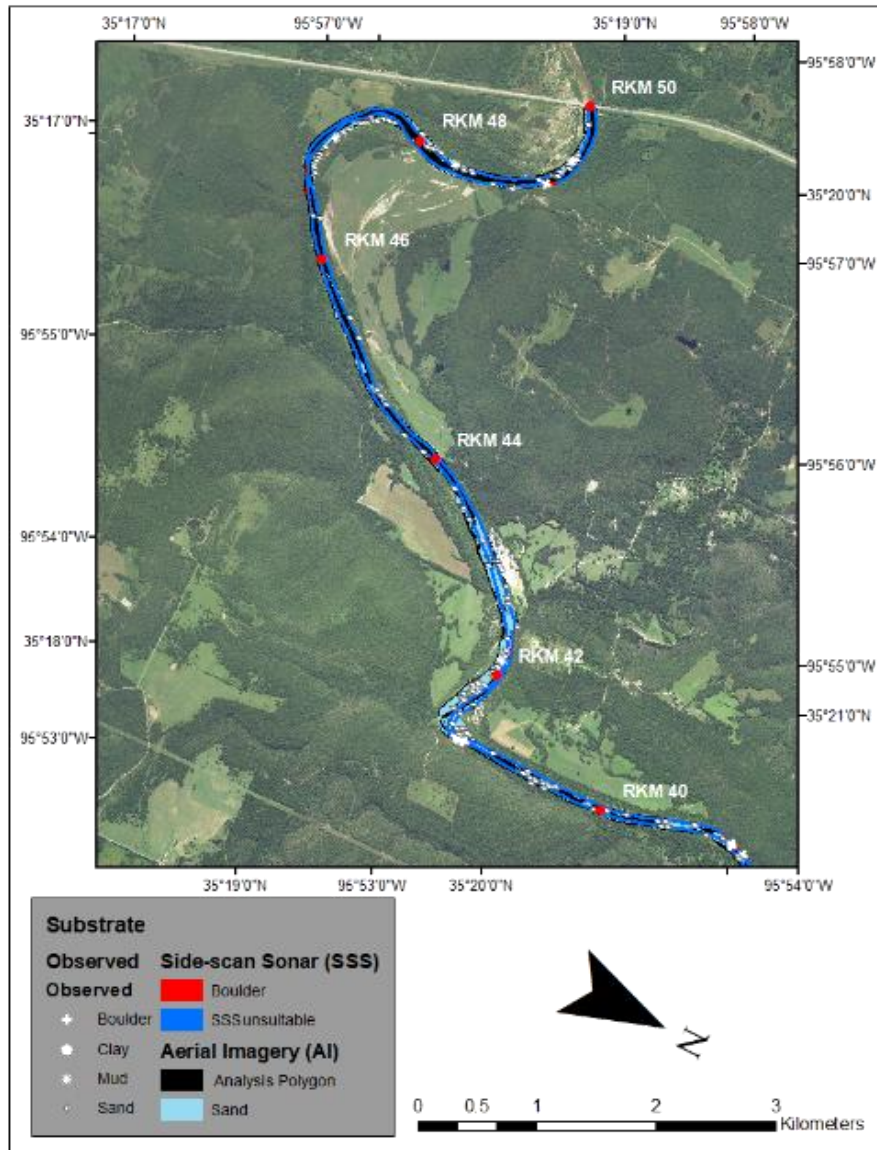


Figure 9.1 Substrate classification maps for the North Canadian River above Lake Eufaula overlaid on 2015 NAIP imagery (National Agriculture Imagery Program). Substrate classifications are grouped according to their method (Aerial imagery (AI) and side-scan sonar (SSS)). Symbols are given for ground truthing points according to the substrate that was found to be present at said point. Maps are listed from upstream to downstream according to river kilometers from the river-reservoir interface of Lake Eufaula.

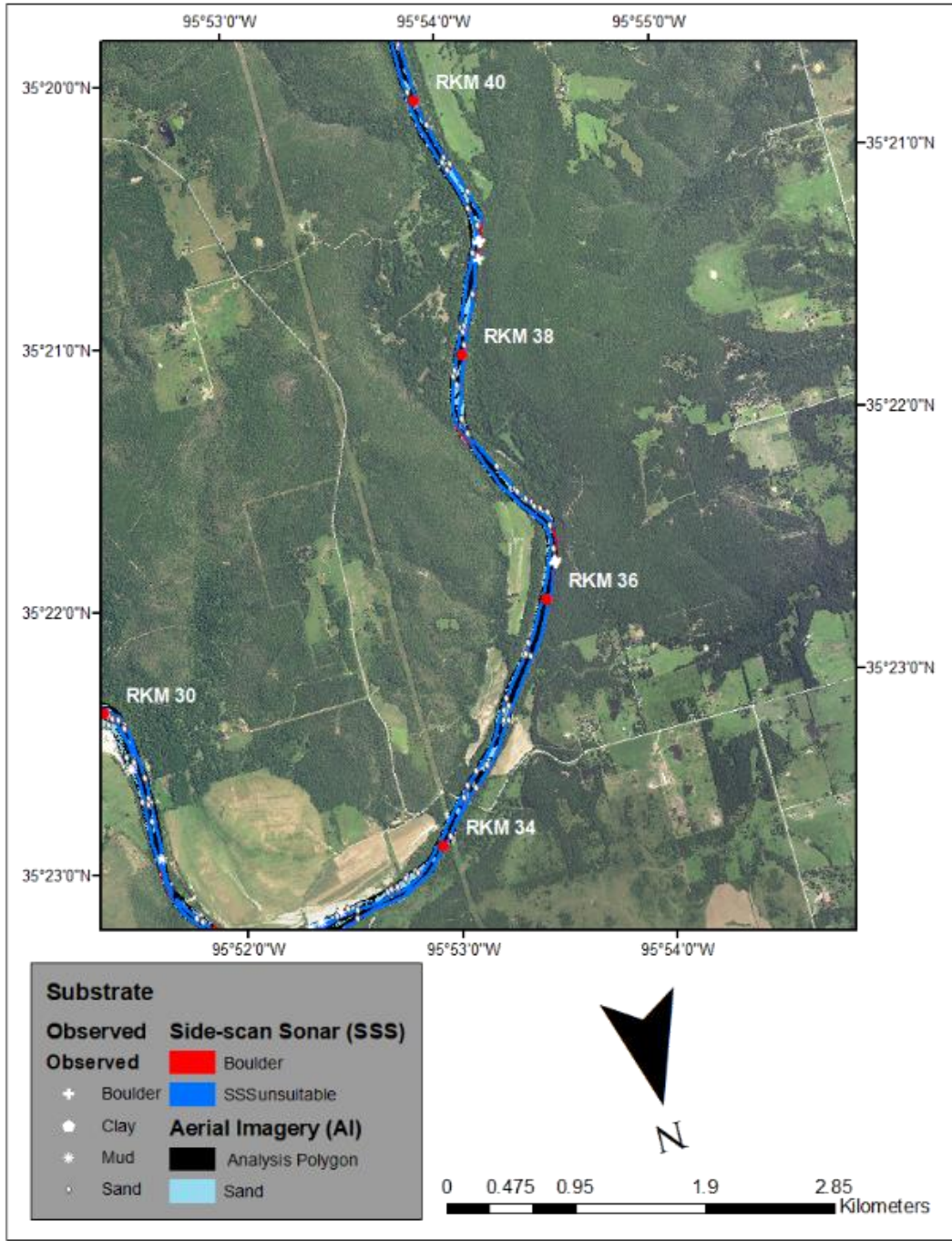


Figure 9.2

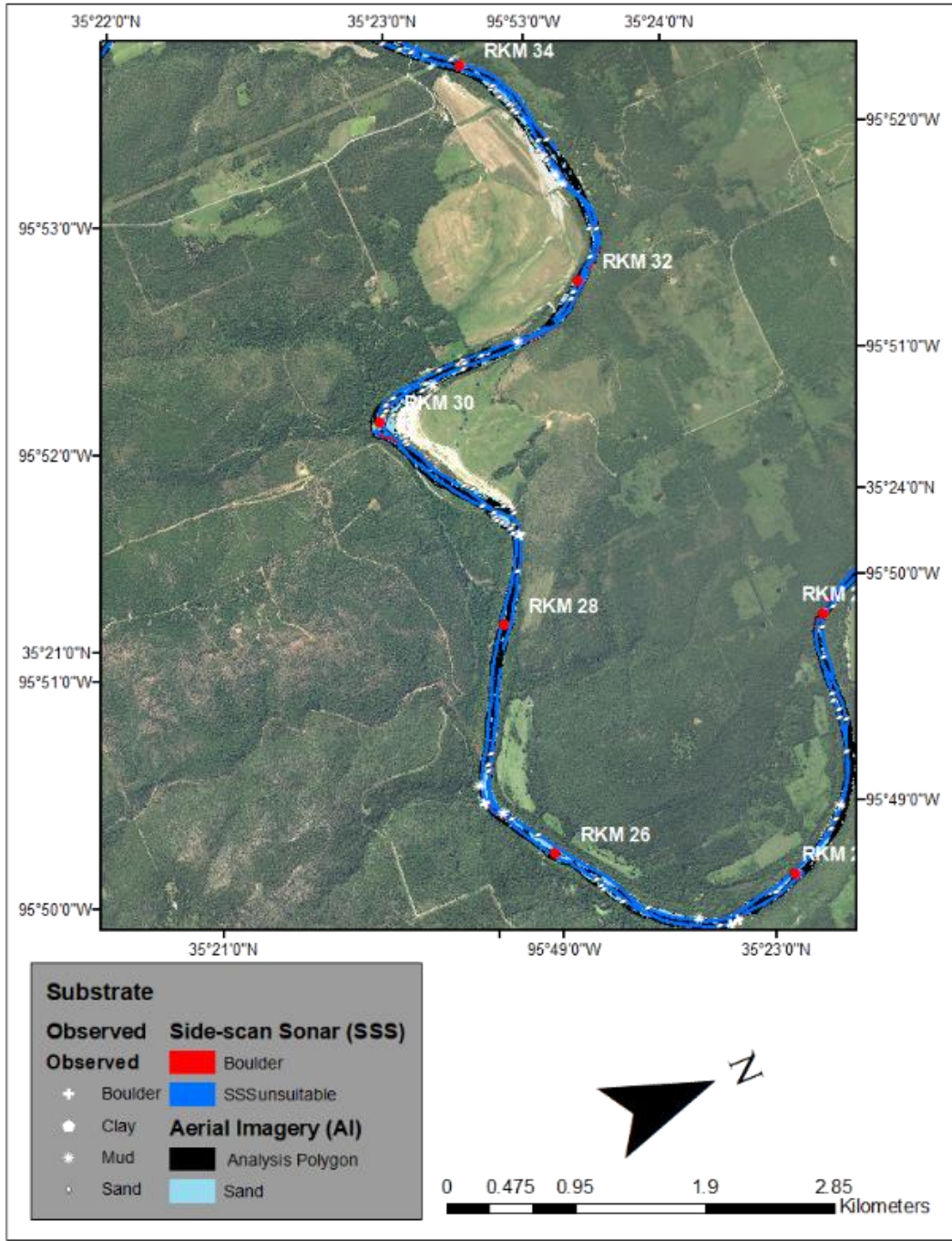


Figure 9.3

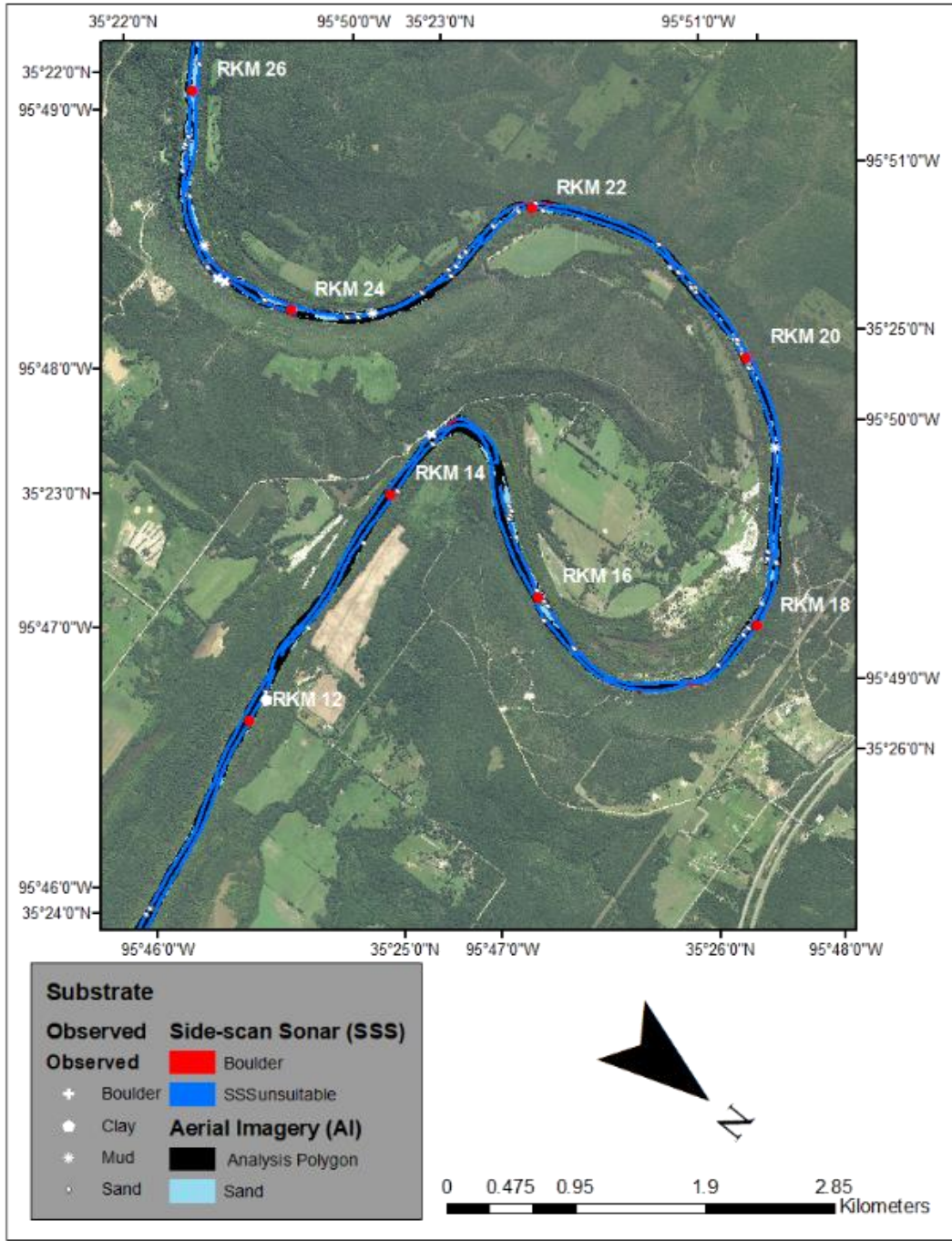


Figure 9.4

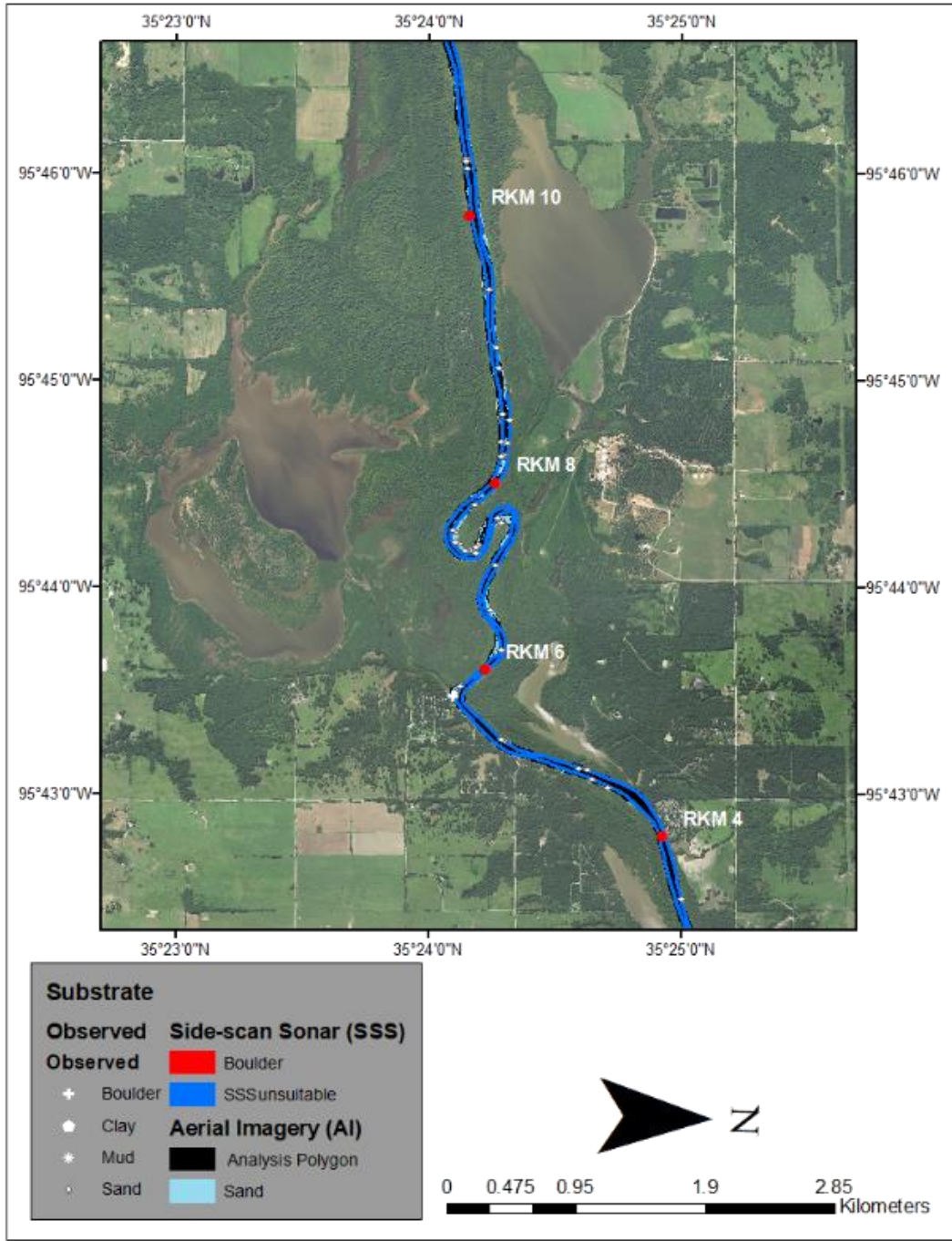


Figure 9.5

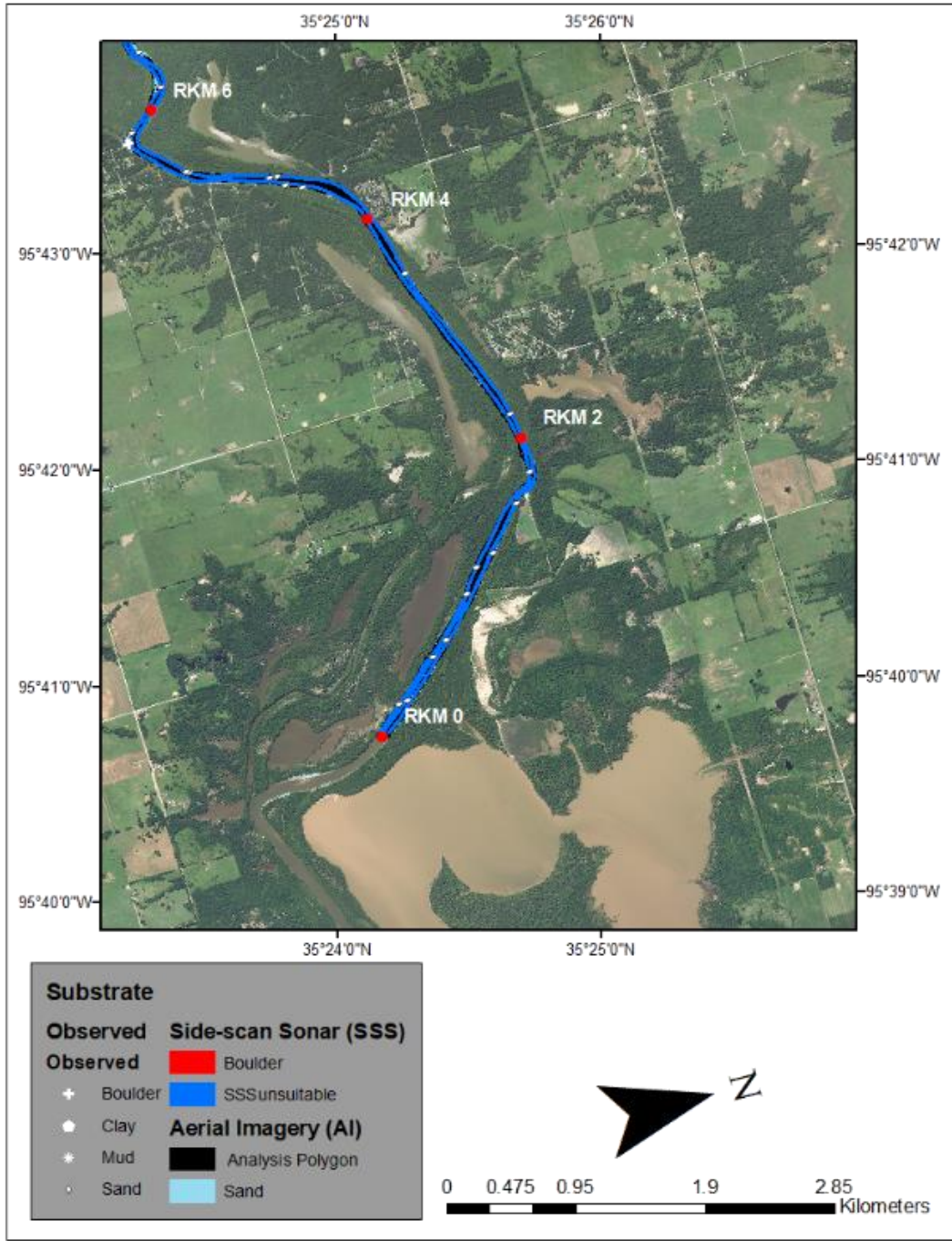


Figure 9.6

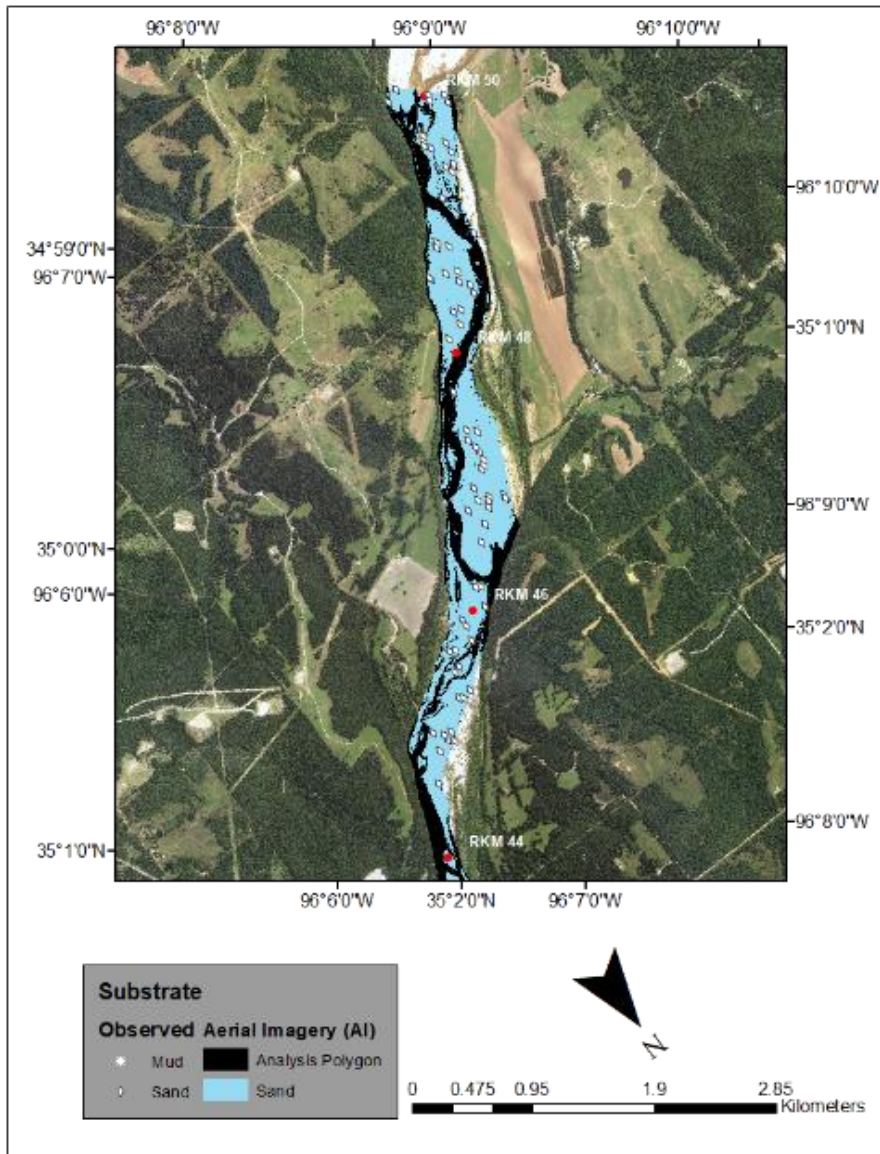


Figure 9.7 Substrate classification maps for the Canadian River above Lake Eufaula overlaid on 2015 NAIP imagery (National Agriculture Imagery Program). Classification of sands substrates are displayed in the polygon that was analyzed by the maximum likelihood method of supervised classification. Symbols are given for ground truthing points according to the substrate that was found to be present at said point. Maps are listed from upstream to downstream according to river kilometers from the river-reservoir interface of Lake Eufaula.

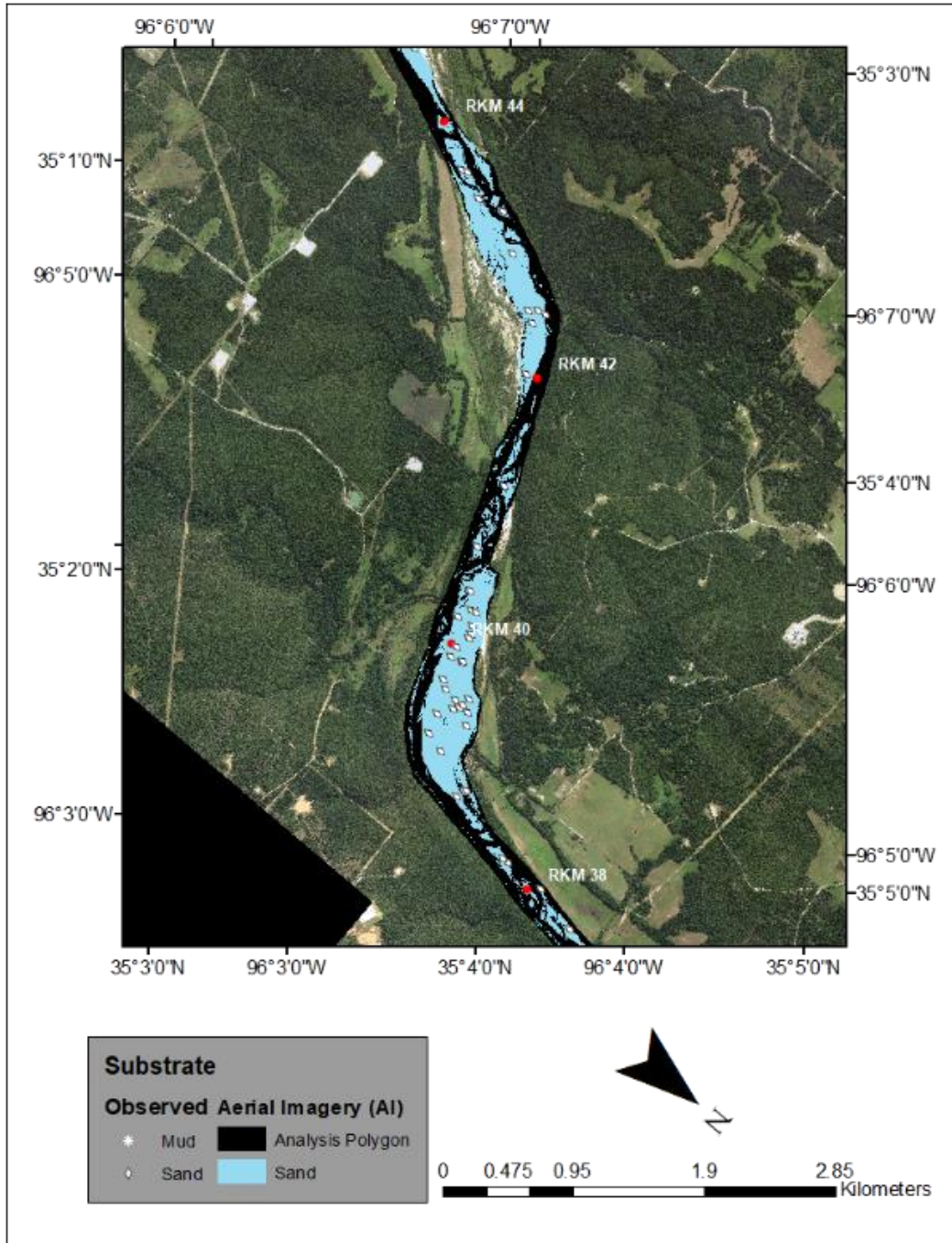


Figure 9.8

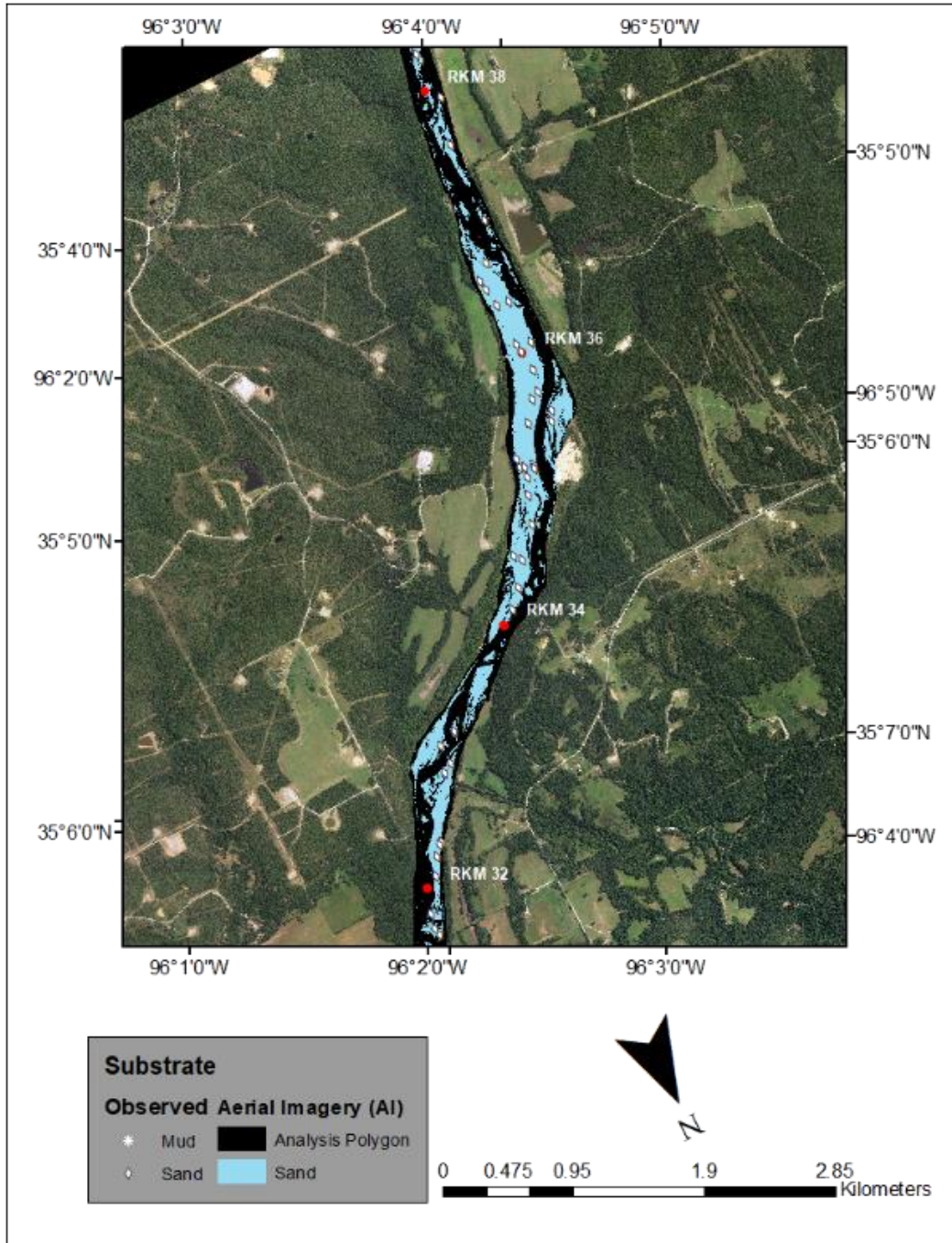


Figure 9.9

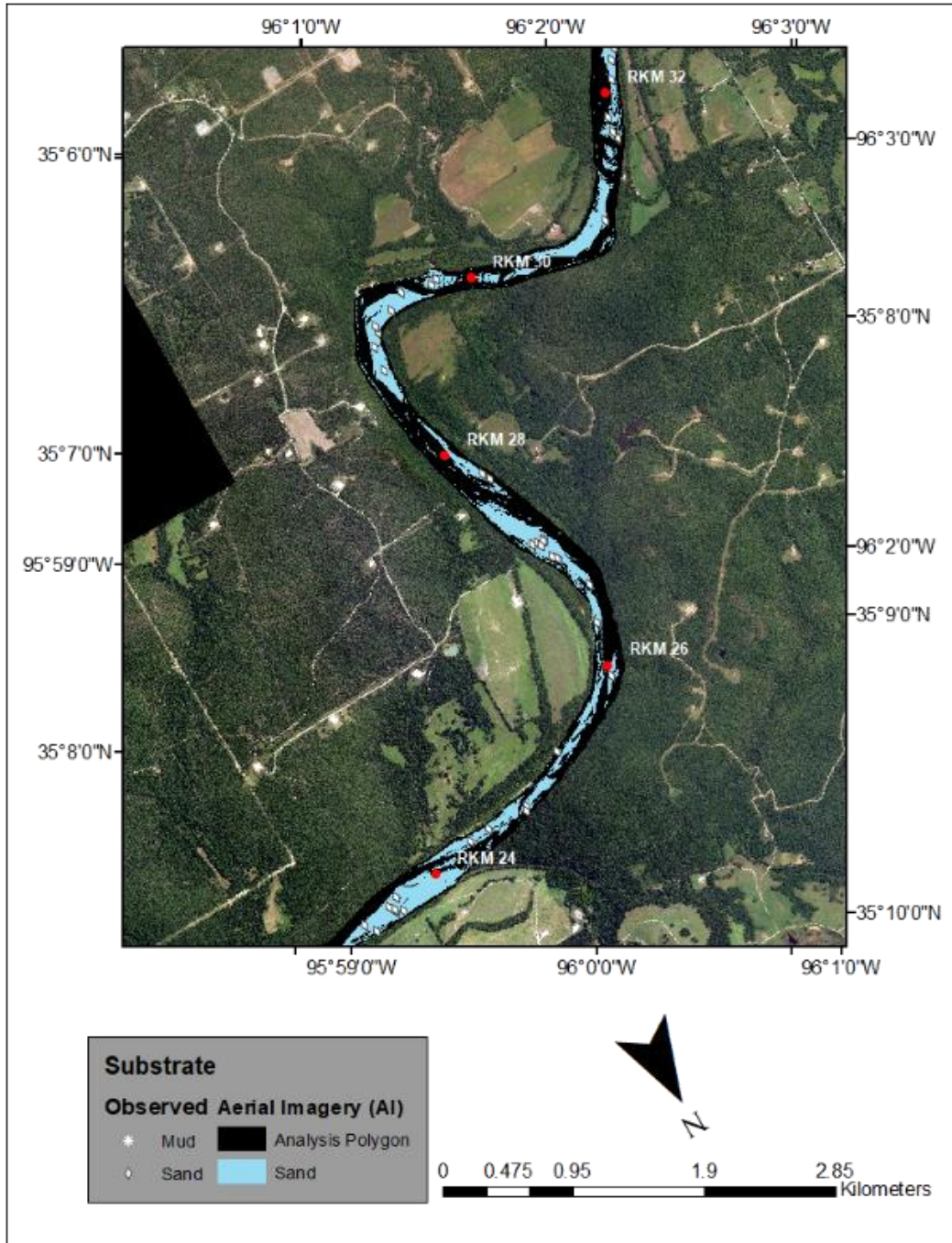


Figure 9.10

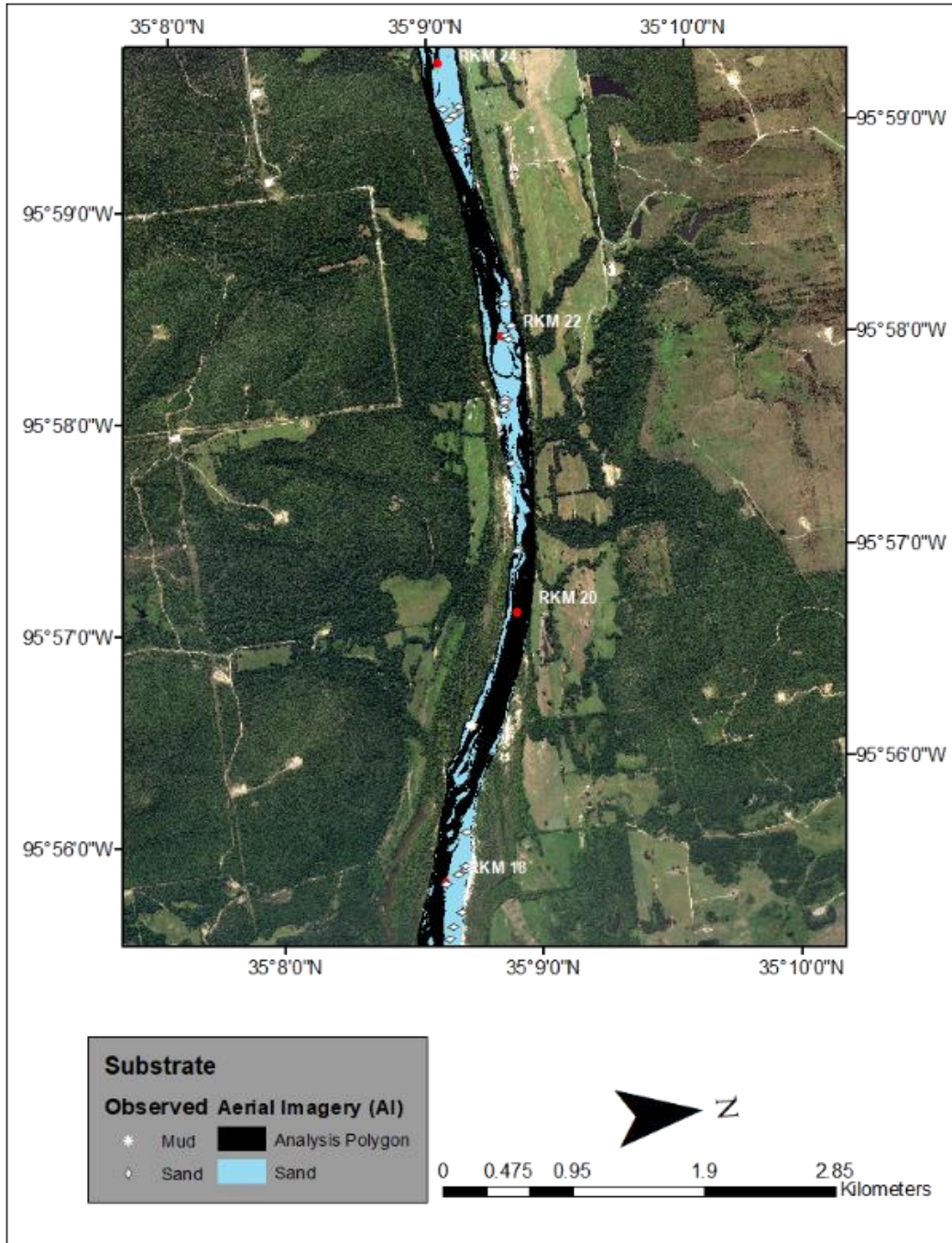


Figure 9.11

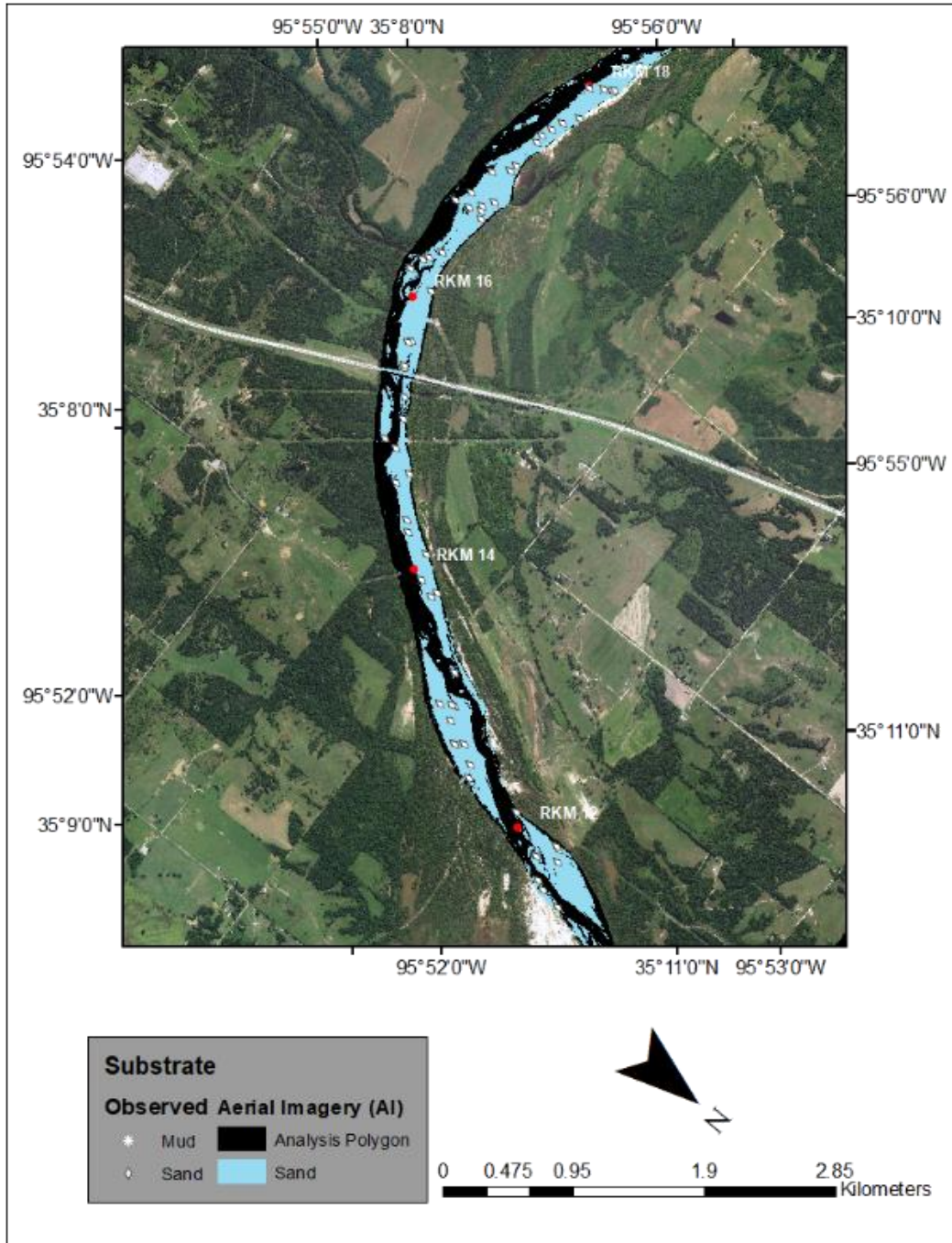


Figure 9.12

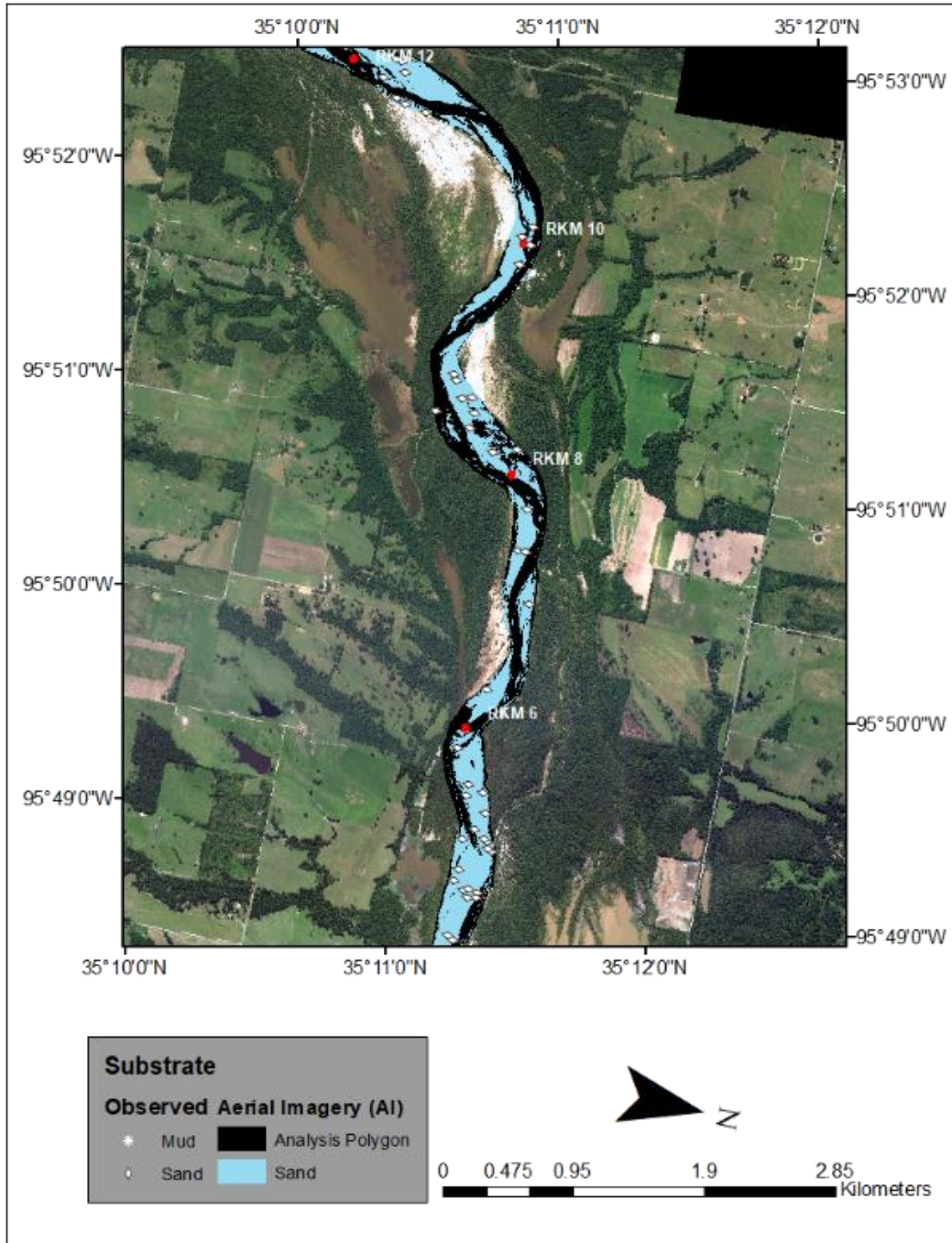


Figure 9.13

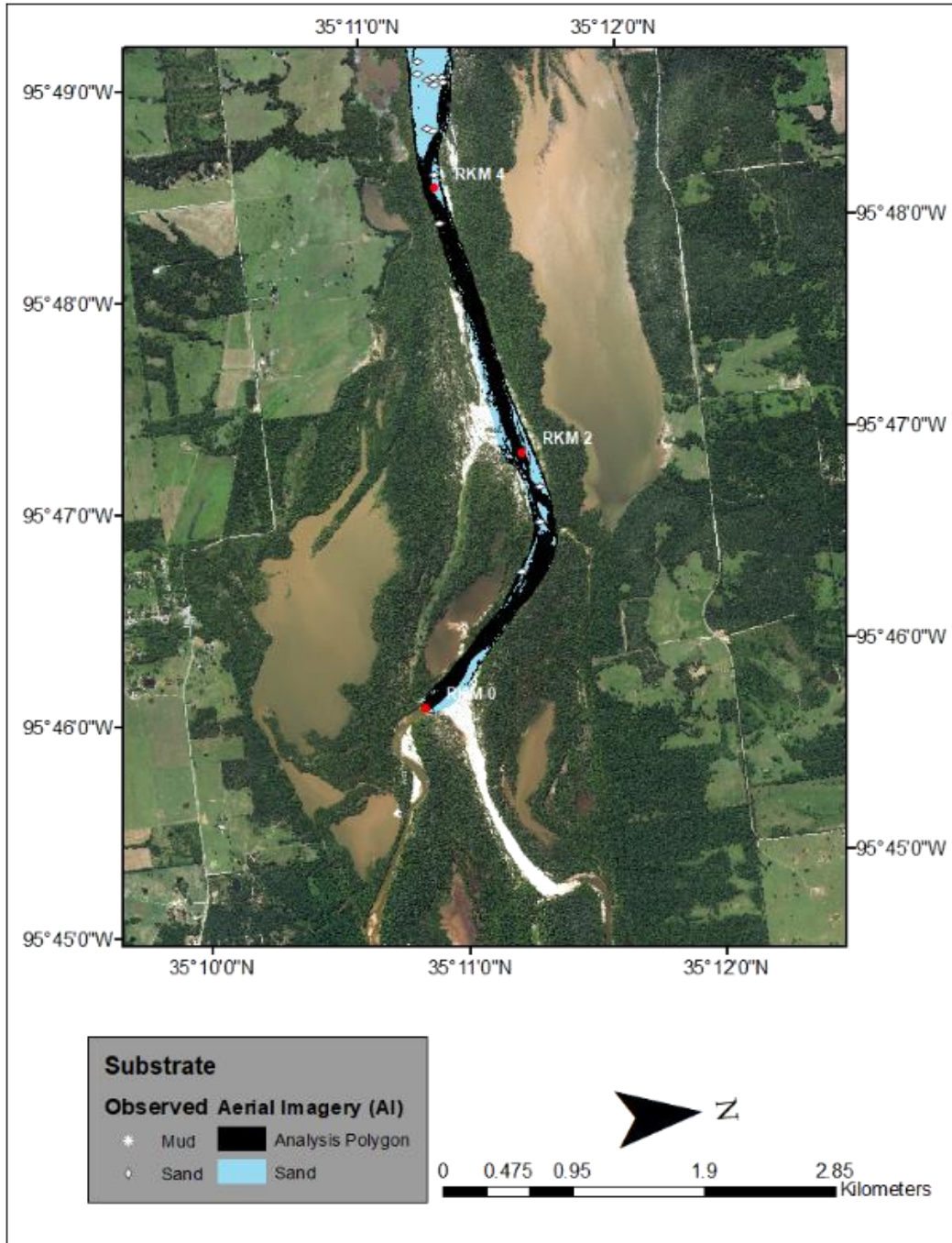


Figure 9.13

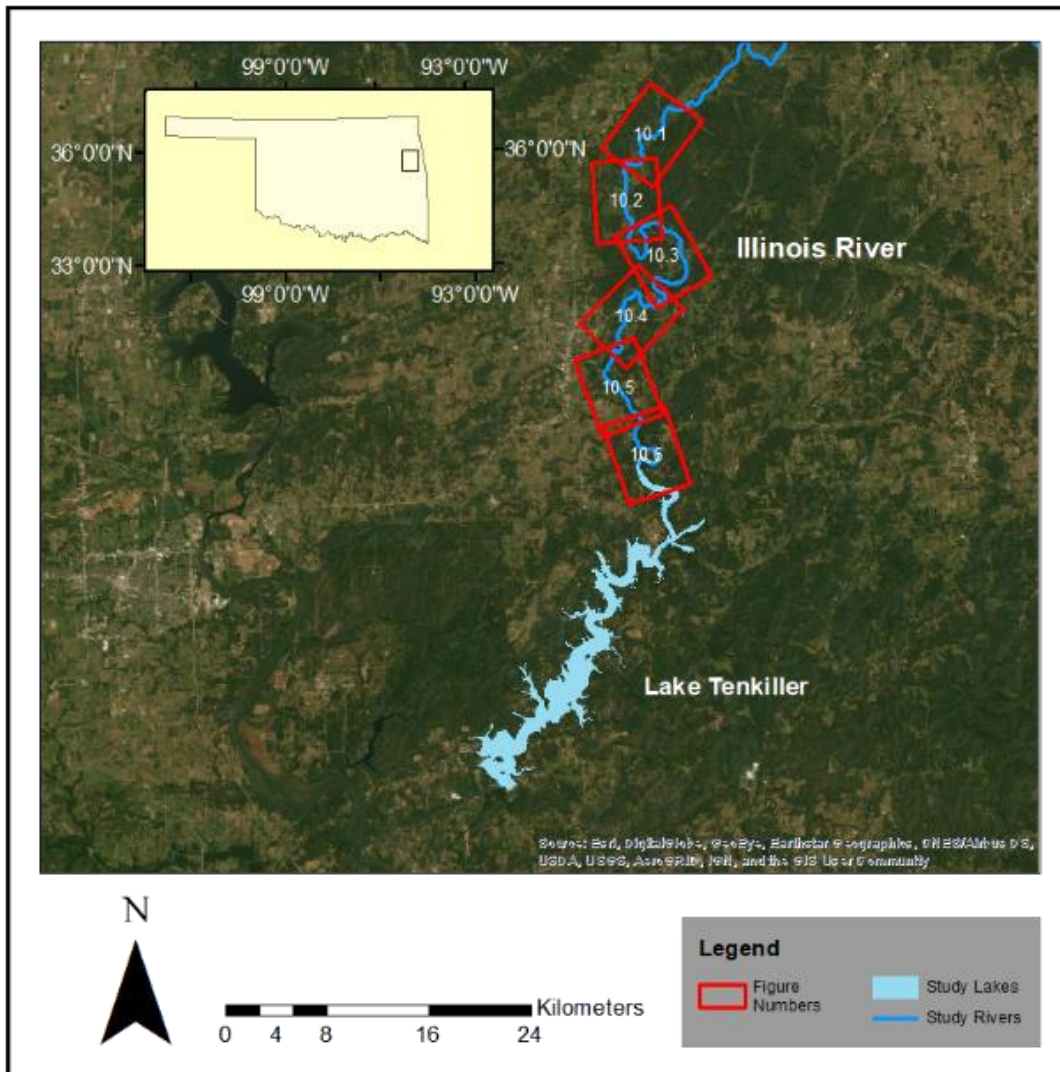


Figure 10. Study area for the Illinois River as a part of the Lake Tenkiller system, overlaid onto USDA aerial imagery in eastern Oklahoma. Higher resolution substrate maps of the Illinois River are depicted in Figures 10.1-10.7, as indicated in red boxes.

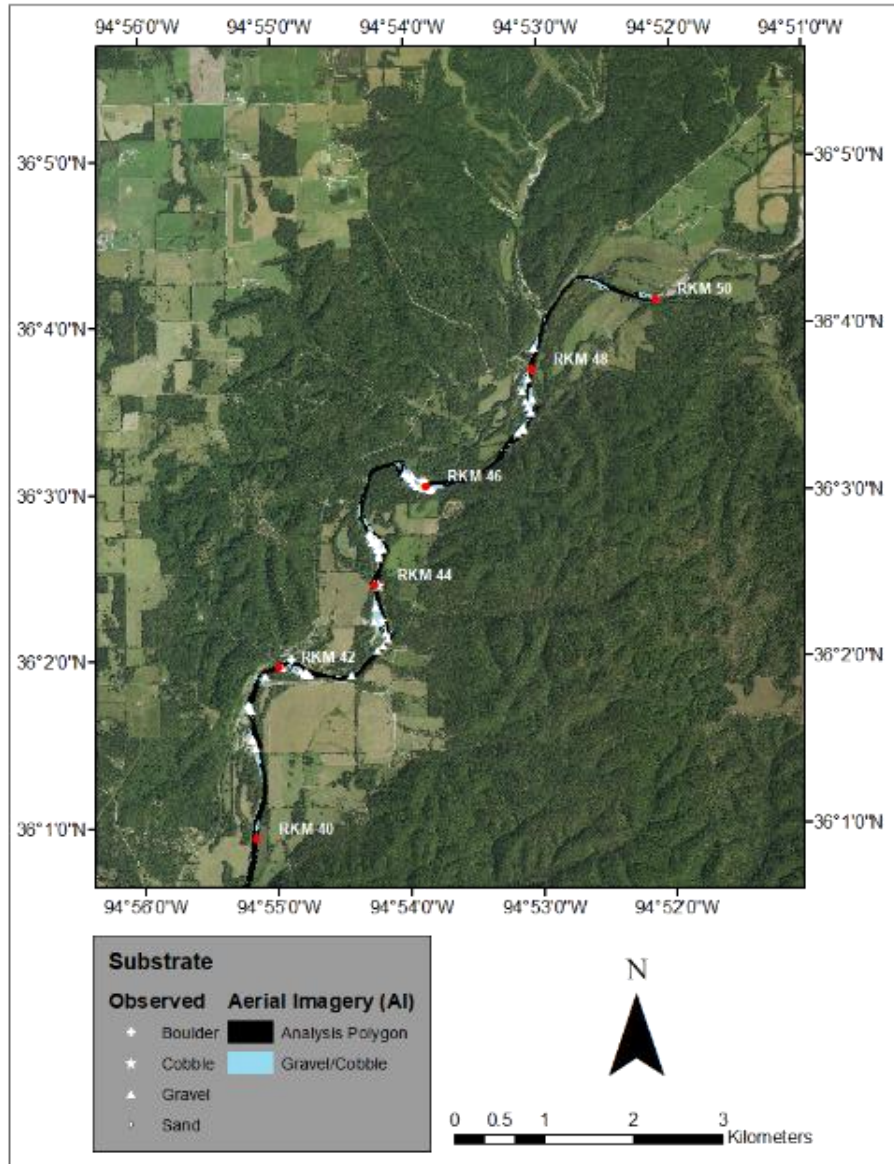
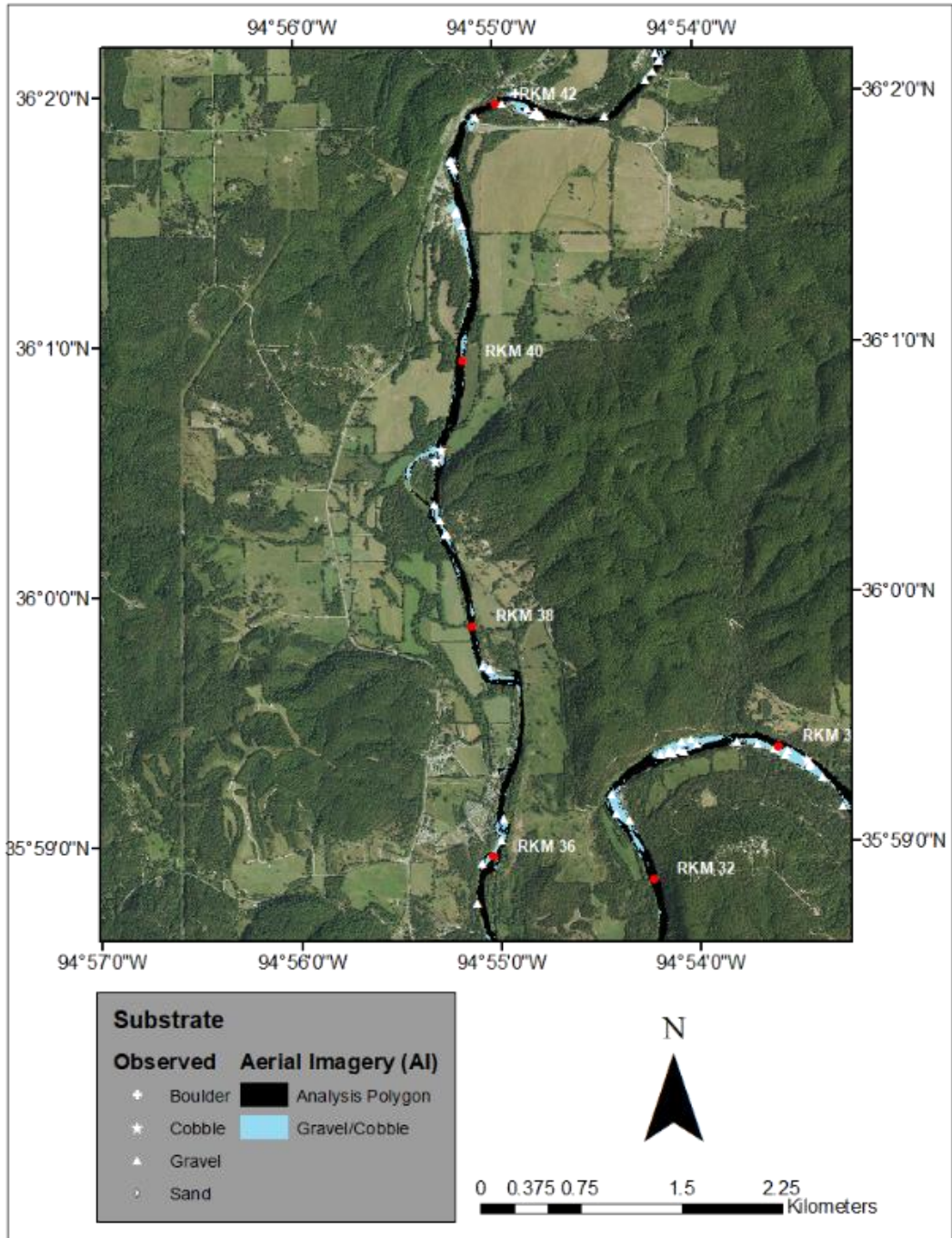
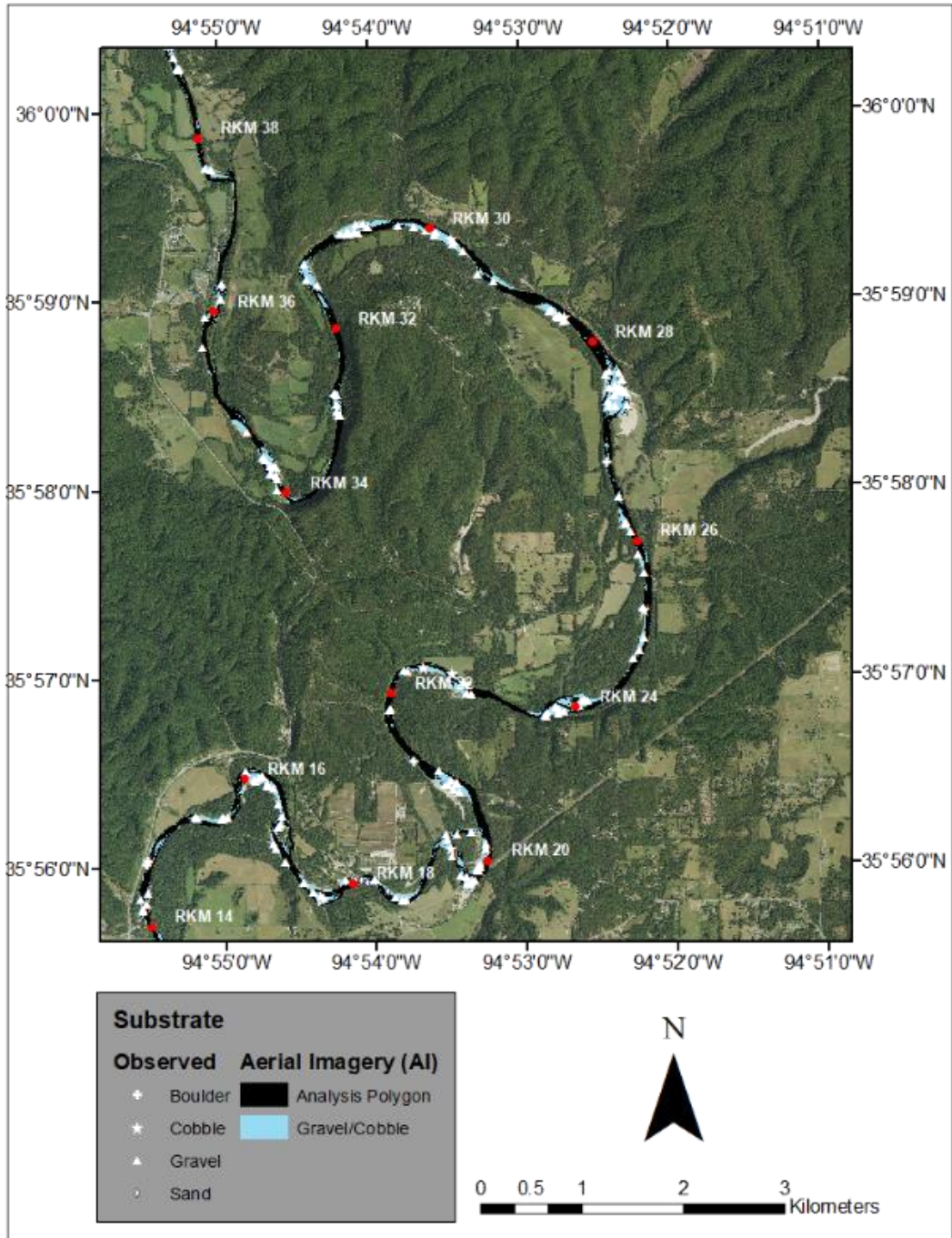
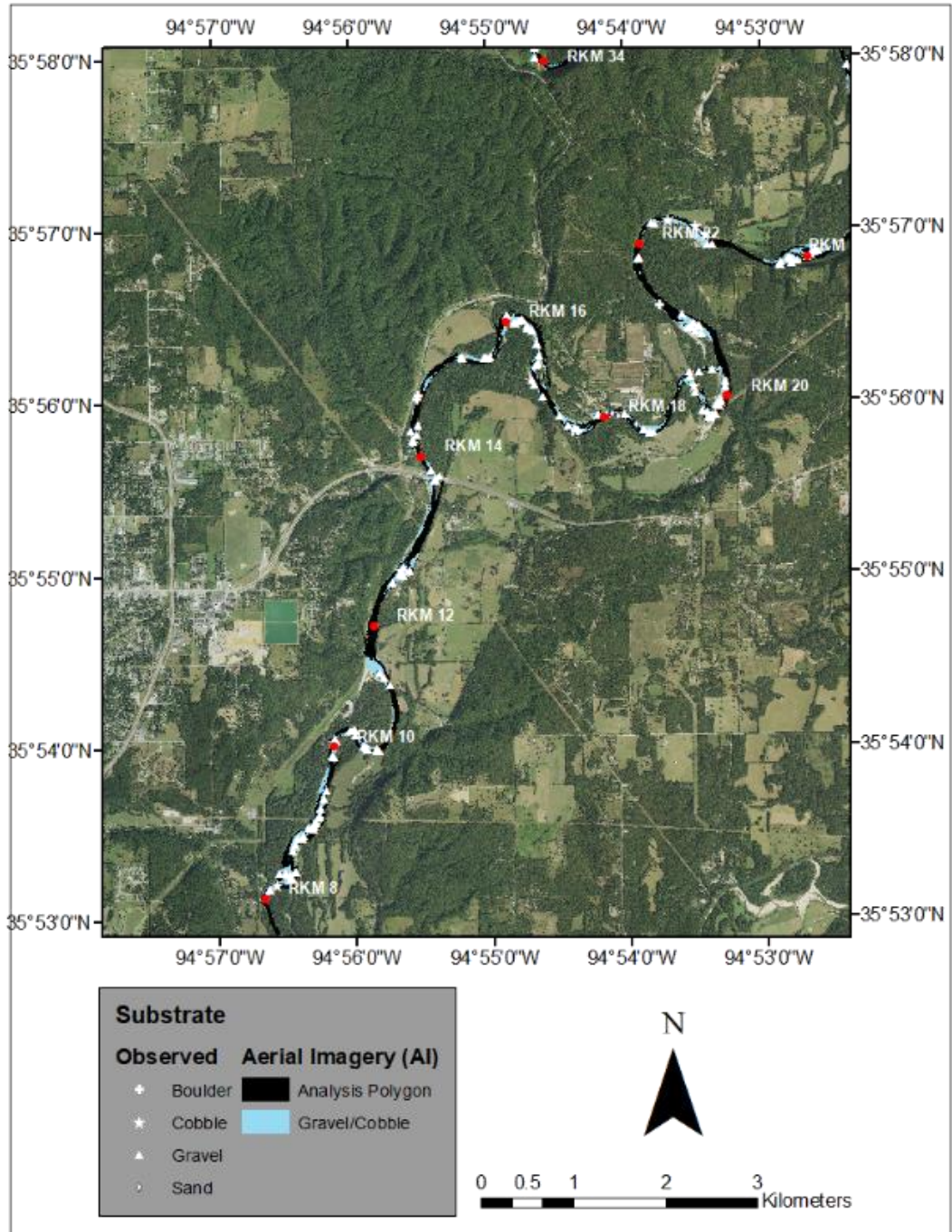
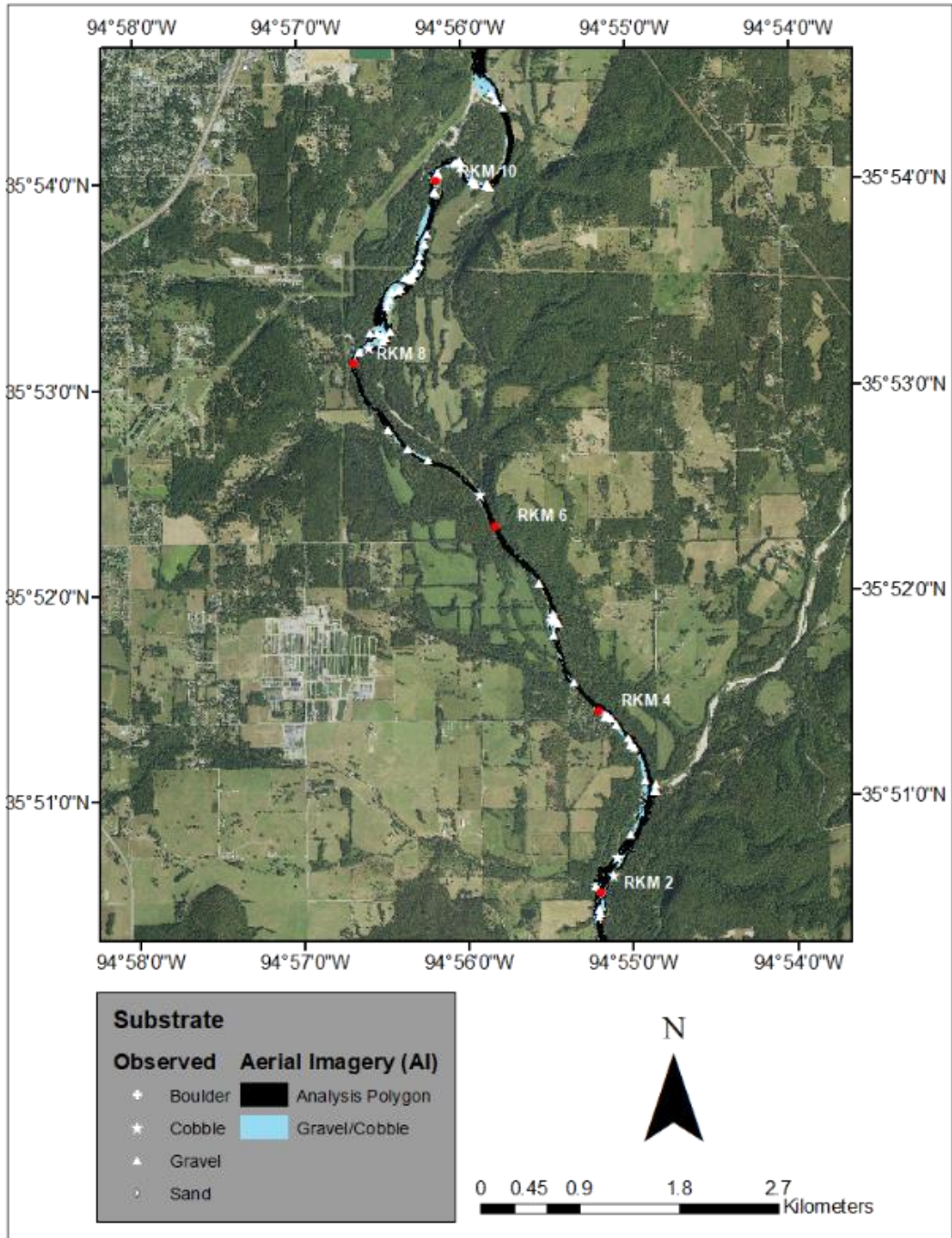


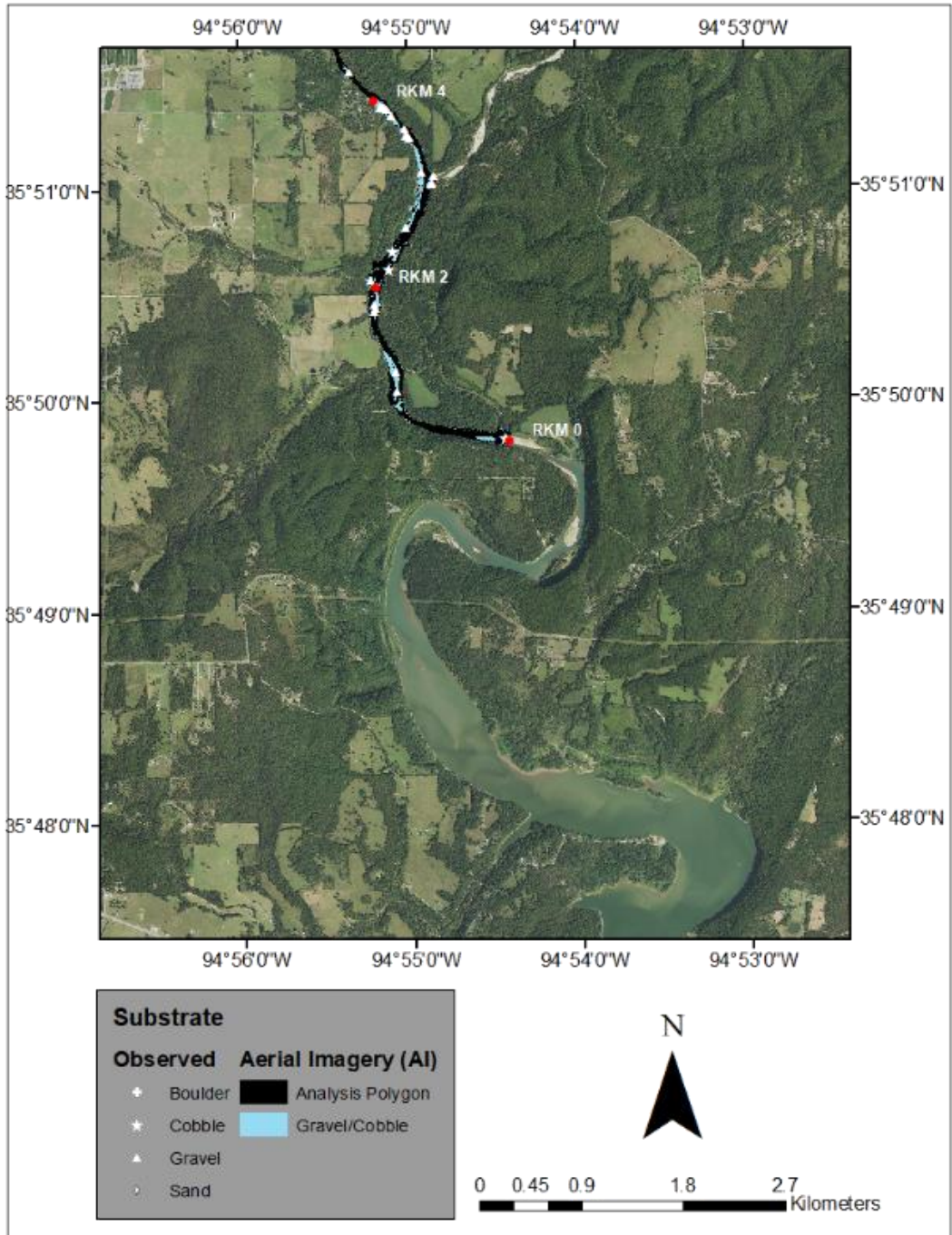
Figure 10.1 Substrate classification maps for the Illinois River above Lake Tenkiller overlaid on 2017 NAIP imagery (National Agriculture Imagery Program). Classification of gravel/cobble substrates are displayed in the polygon that was analyzed by the maximum likelihood method of supervised classification. Symbols are given for ground truthing points according to the substrate that was found to be present at said point. Maps are listed from upstream to downstream according to river kilometers from the river-reservoir interface of Lake Tenkiller.











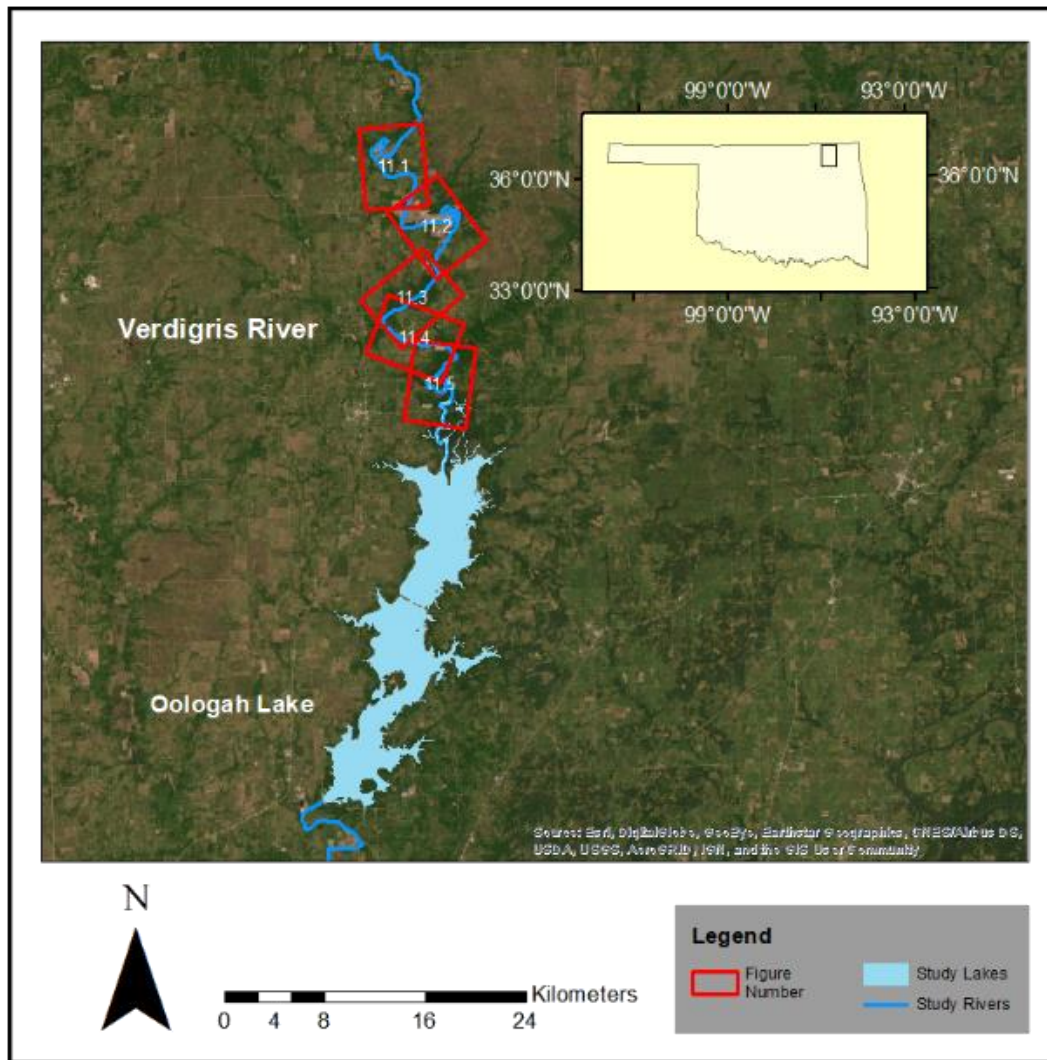


Figure 11. Study area for the Verdigris River as a part of the Oologah Lake system, overlaid onto USDA aerial imagery in northeast Oklahoma. Higher resolution substrate maps of the Verdigris River are depicted in Figures 11.1-11.5, as indicated in red boxes.

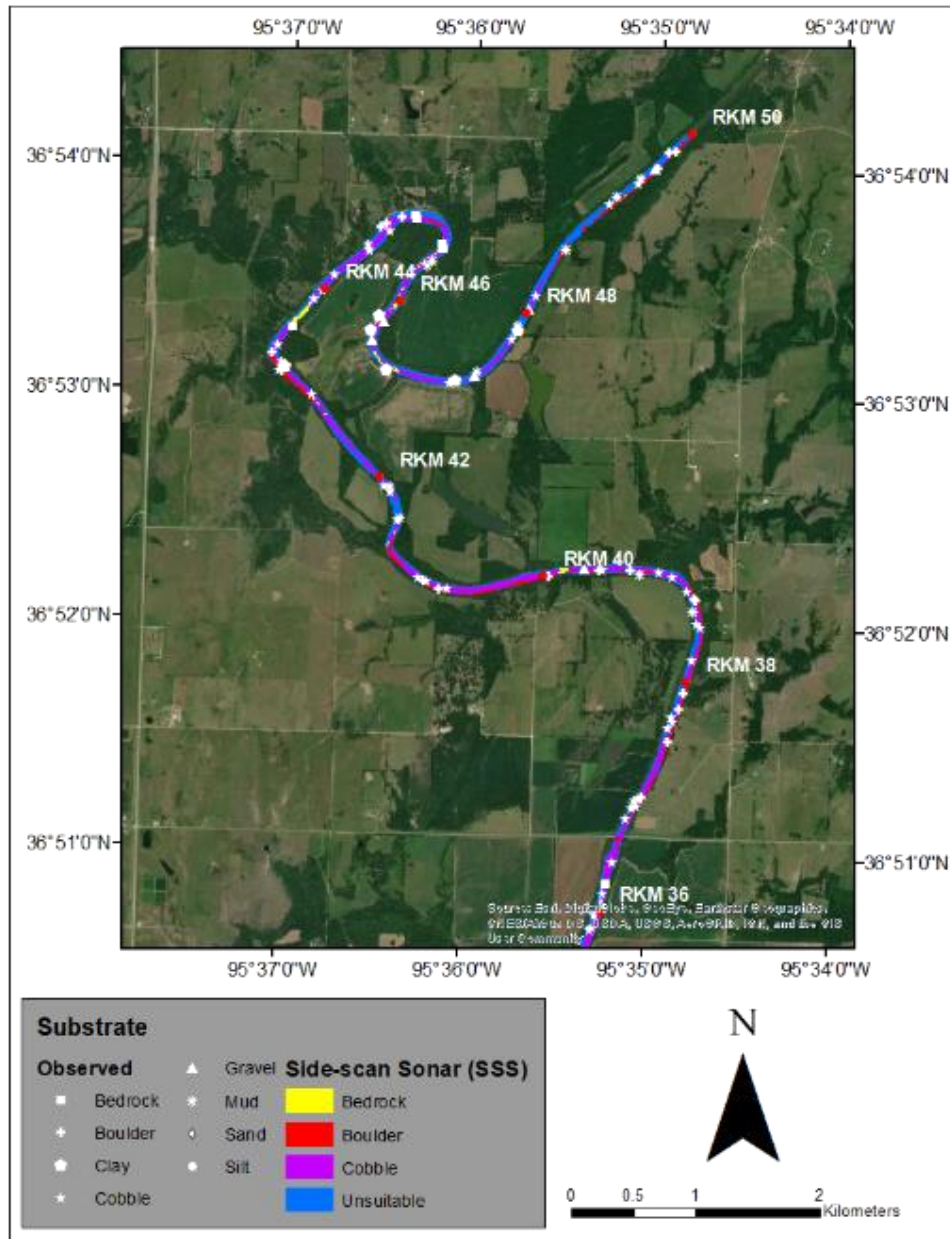


Figure 11.1 Substrate classification maps for the Verdigris River overlaid on USDA aerial imagery. Substrates are classified by unsuitable or type of suitable substrate as determined by side-scan sonar. Symbols are given for ground truthing points according to the substrate that was found to be present at said point. Maps are listed from upstream to downstream according to river kilometers from the river-reservoir interface of Oologah Lake.

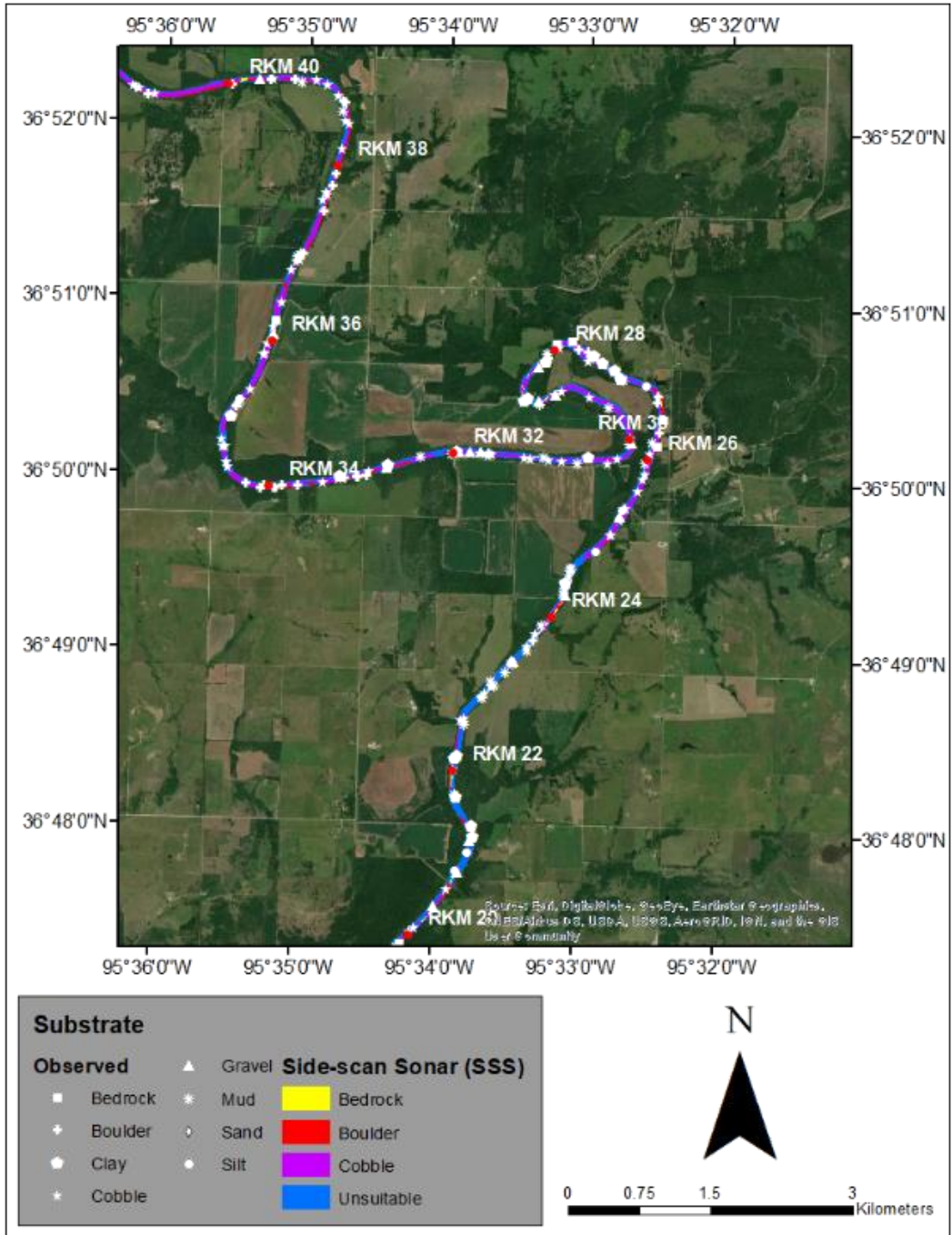


Figure 11.2

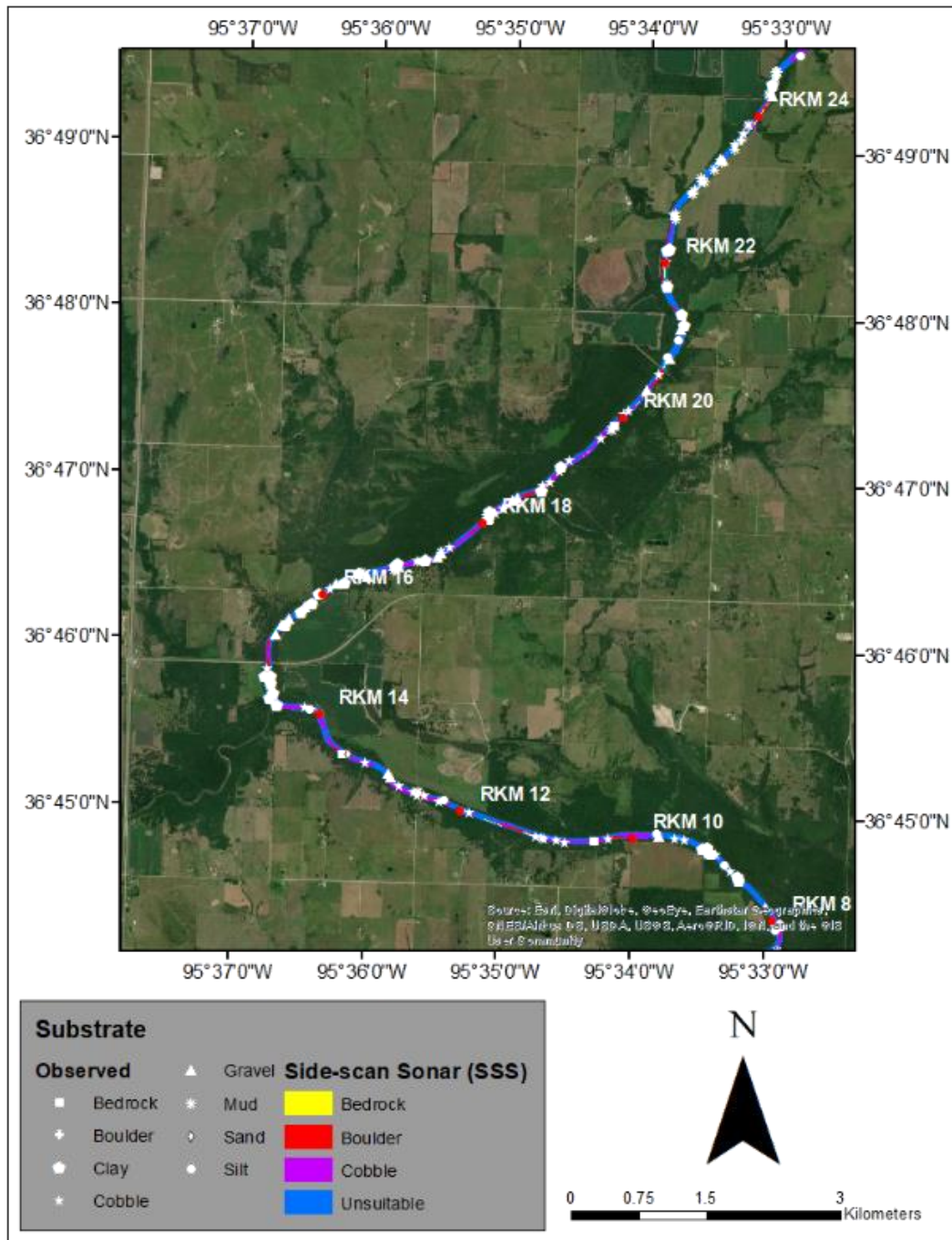


Figure 11.3

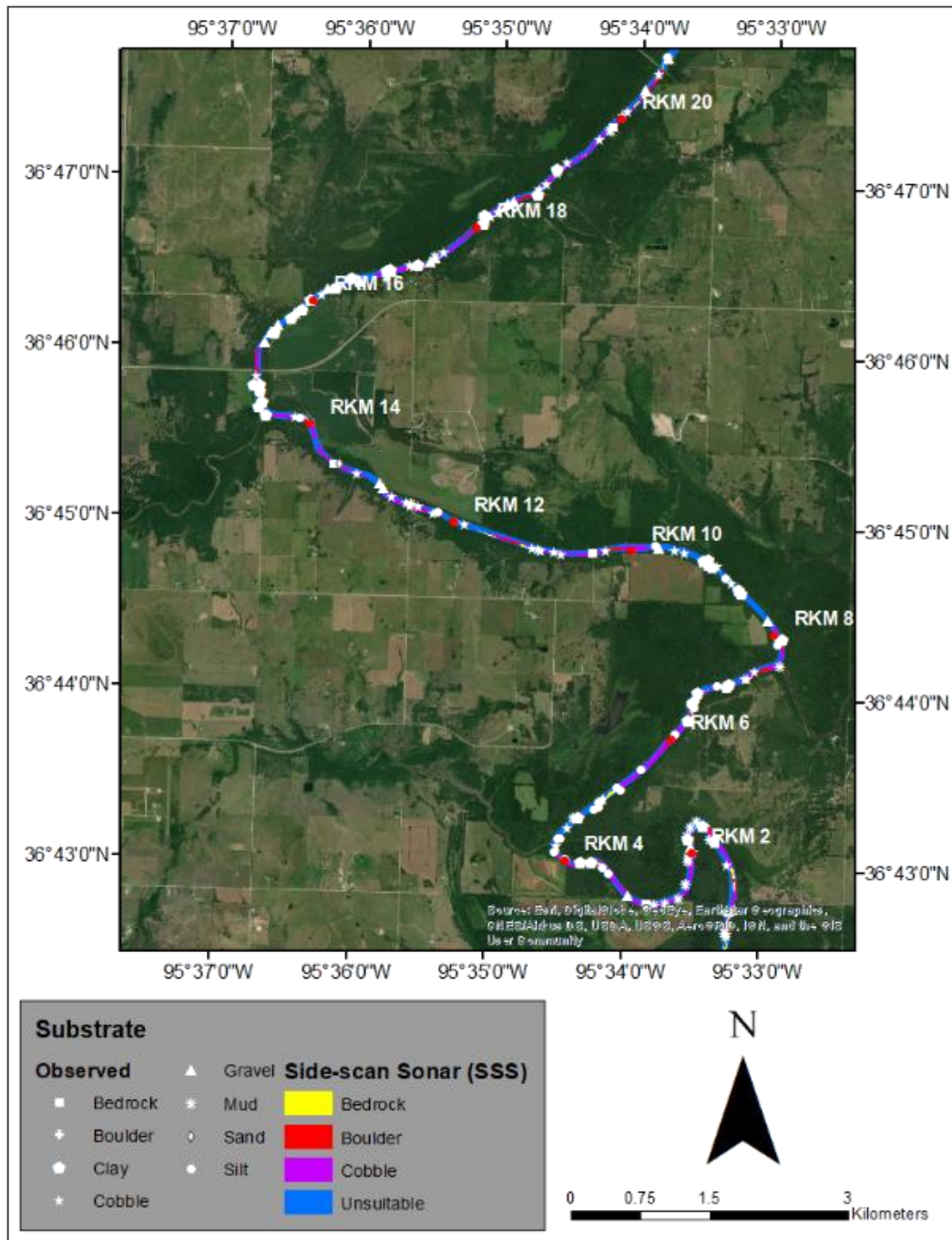


Figure 11.4

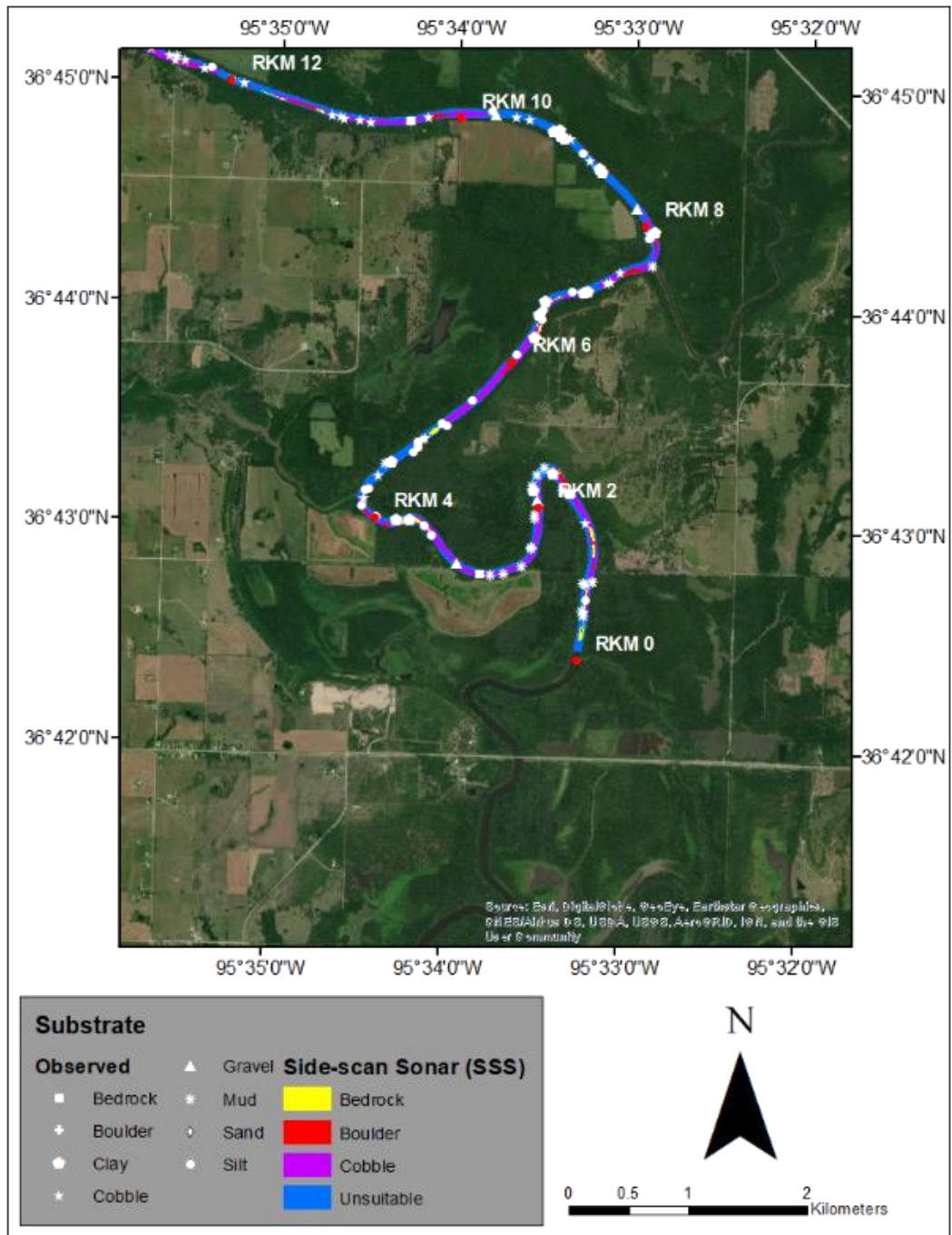


Figure 11.5

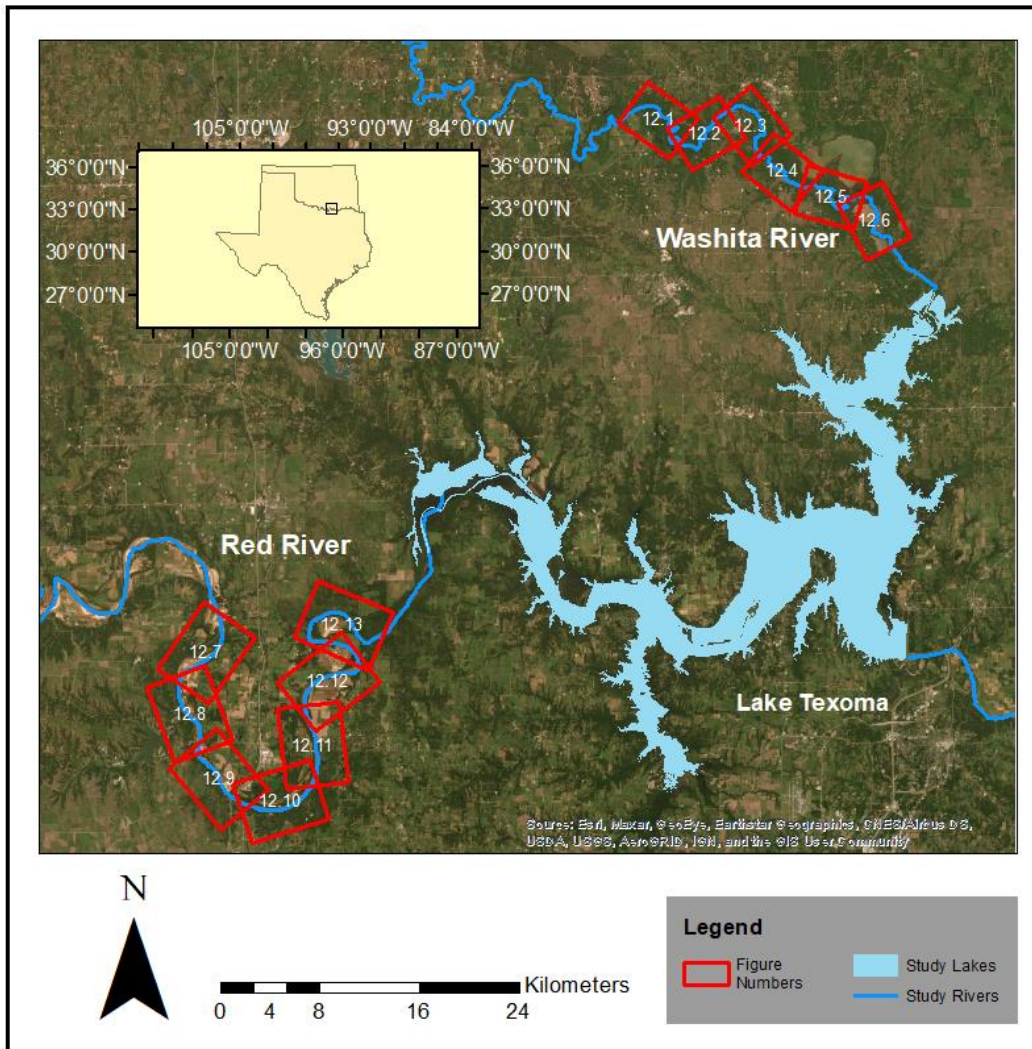


Figure 12. Study area for the Washita and Red rivers as a part of the Lake Texoma system, overlaid onto USDA aerial imagery on the Oklahoma/Texas border. Higher resolution substrate maps of the Washita and Red rivers are depicted in Figures 12.1-12.13, as indicated in red boxes.

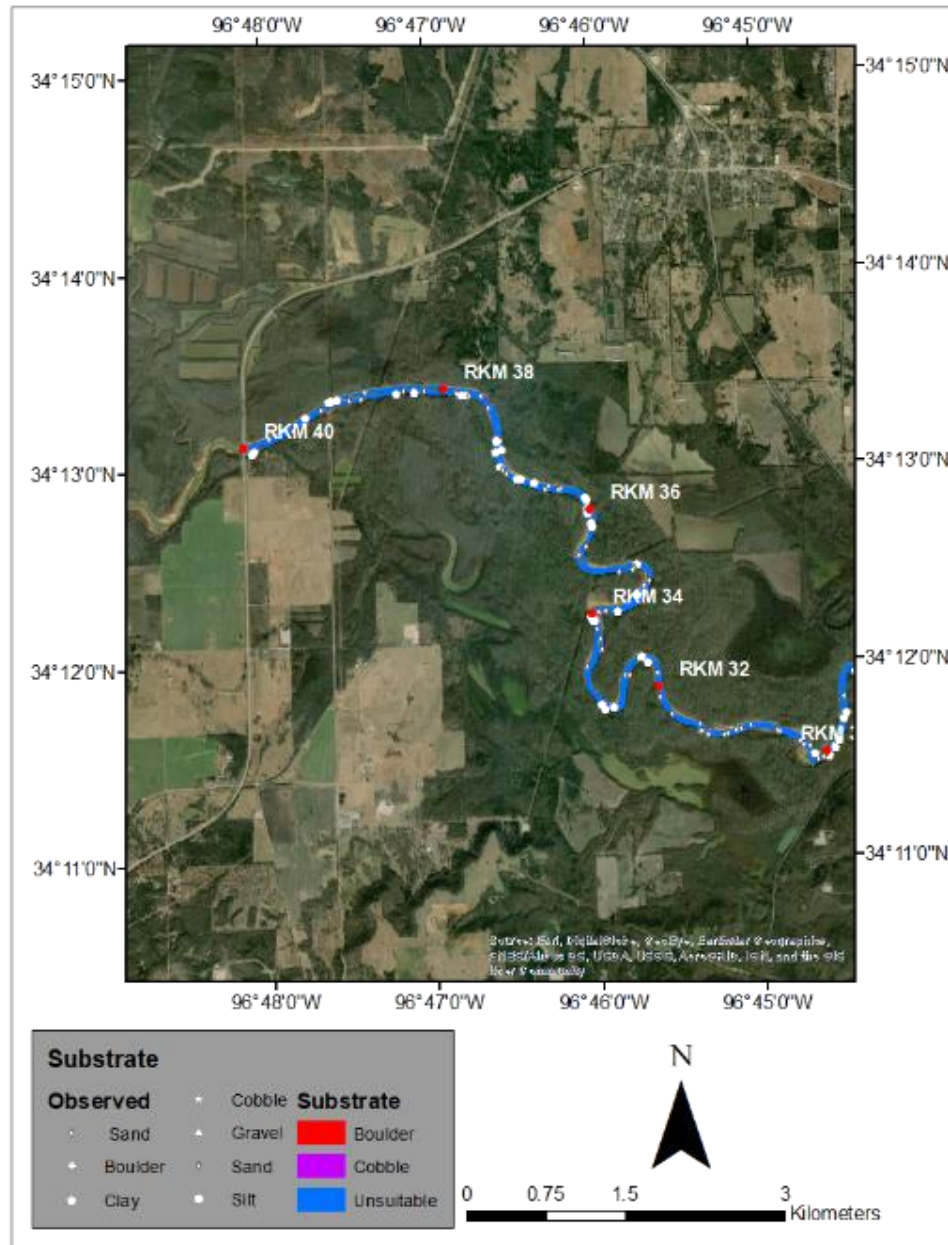


Figure 12.1 Substrate classification maps for the Washita River overlaid on USDA aerial imagery. Substrates are classified by unsuitable or type of suitable substrate as determined by side-scan sonar. Symbols are given for ground truthing points according to the substrate that was found to be present at said point. Maps are listed from upstream to downstream according to river kilometers from the river-reservoir interface of Lake Texoma.

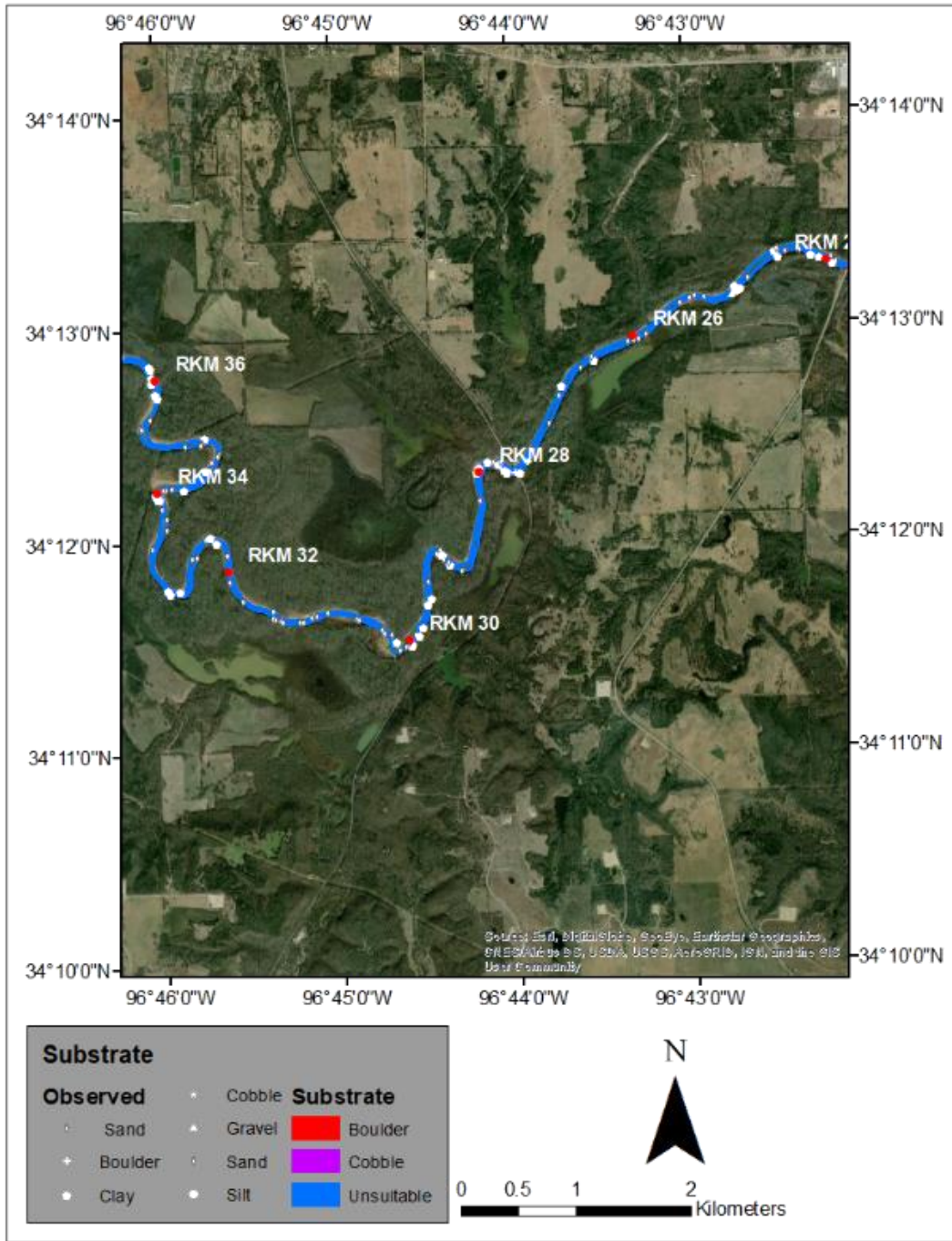


Figure 12.2

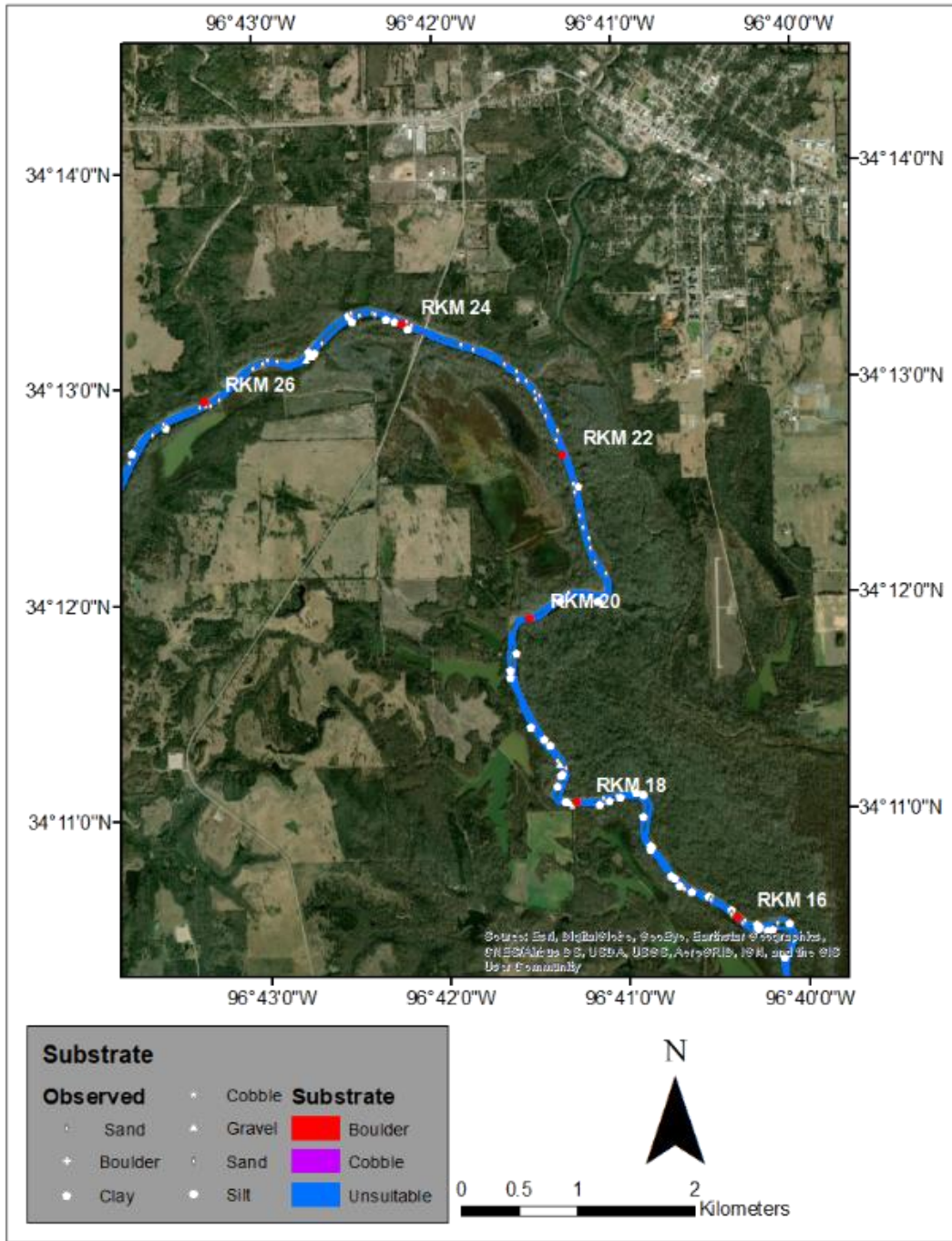


Figure 12.3

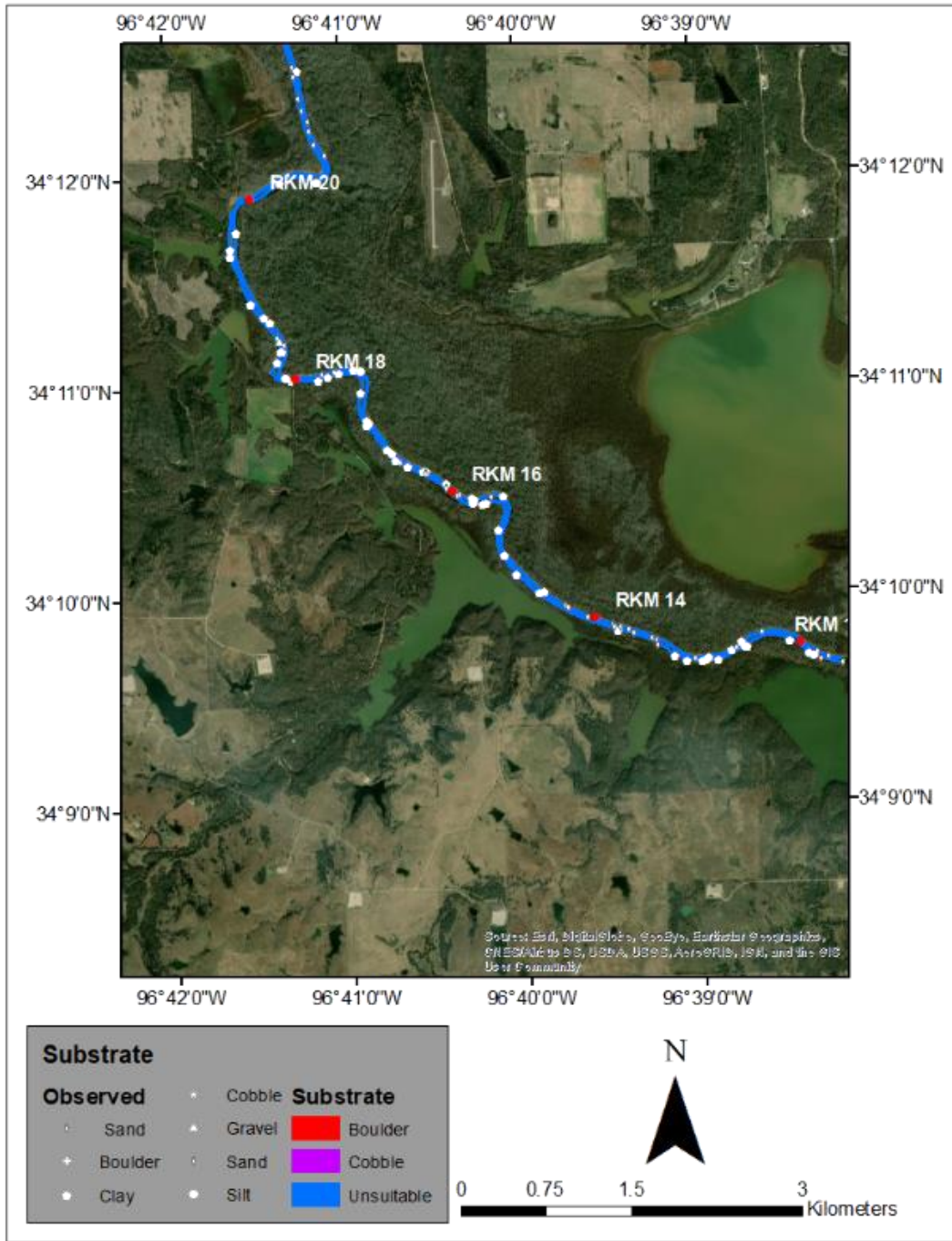


Figure 12.4

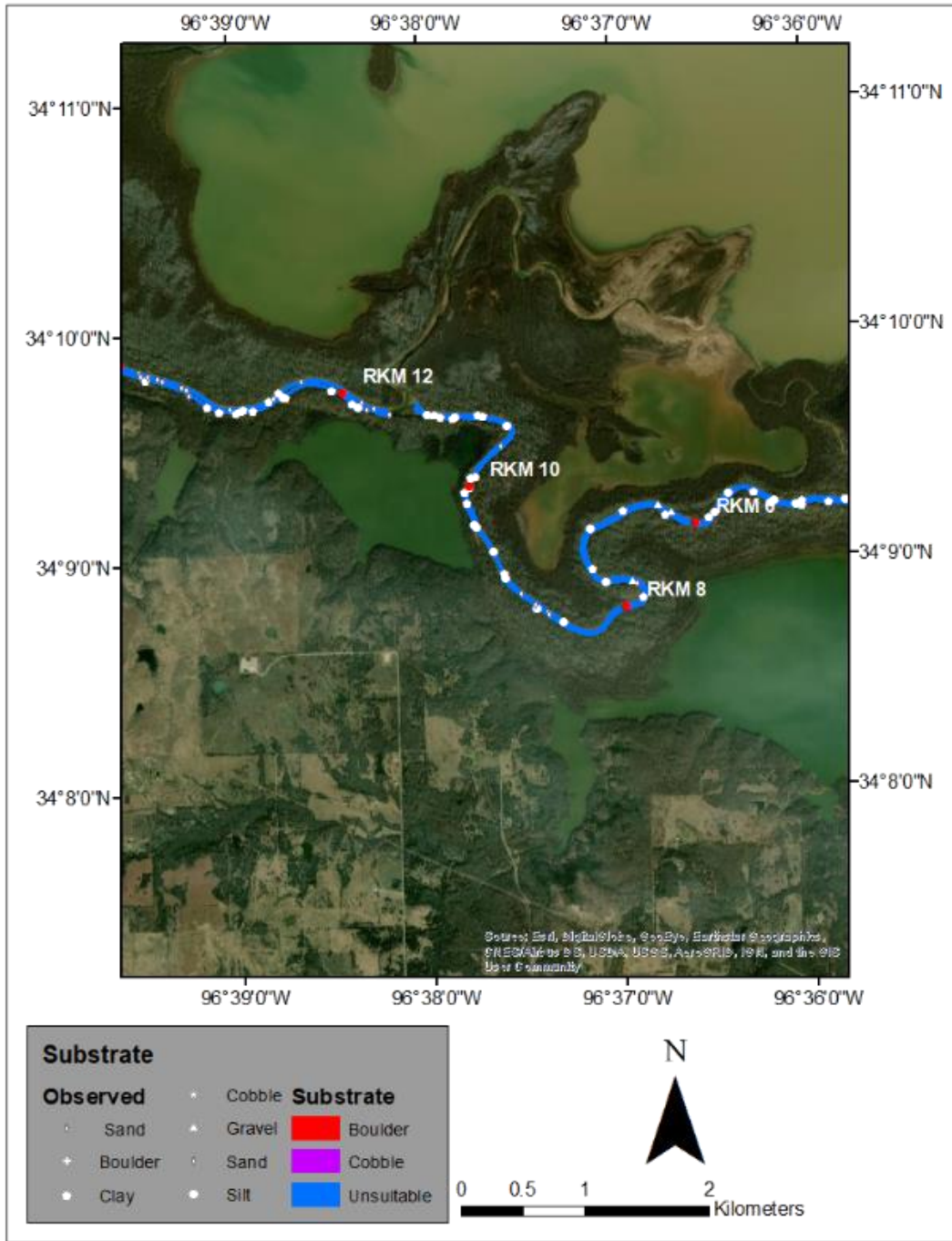


Figure 12.5

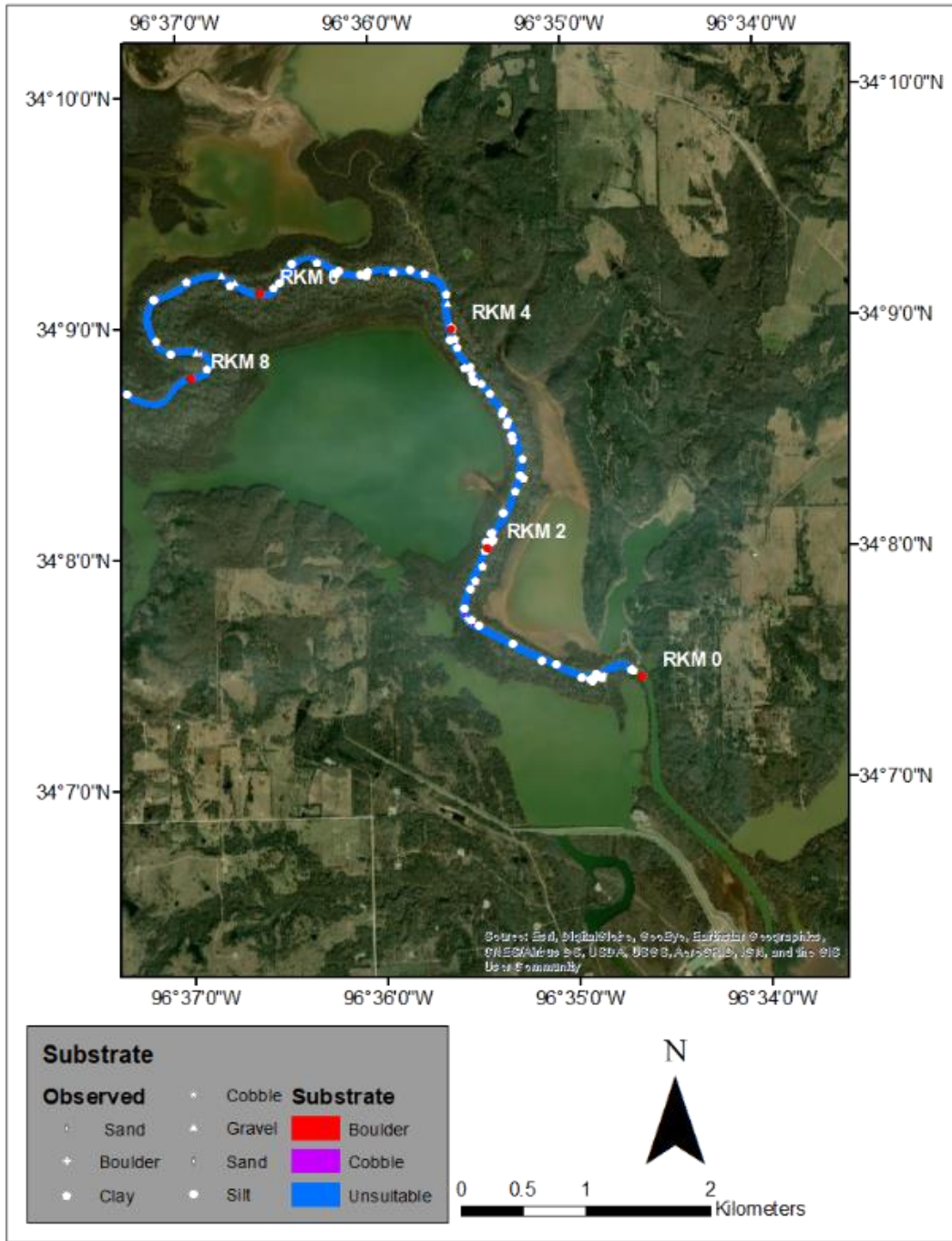


Figure 12.6

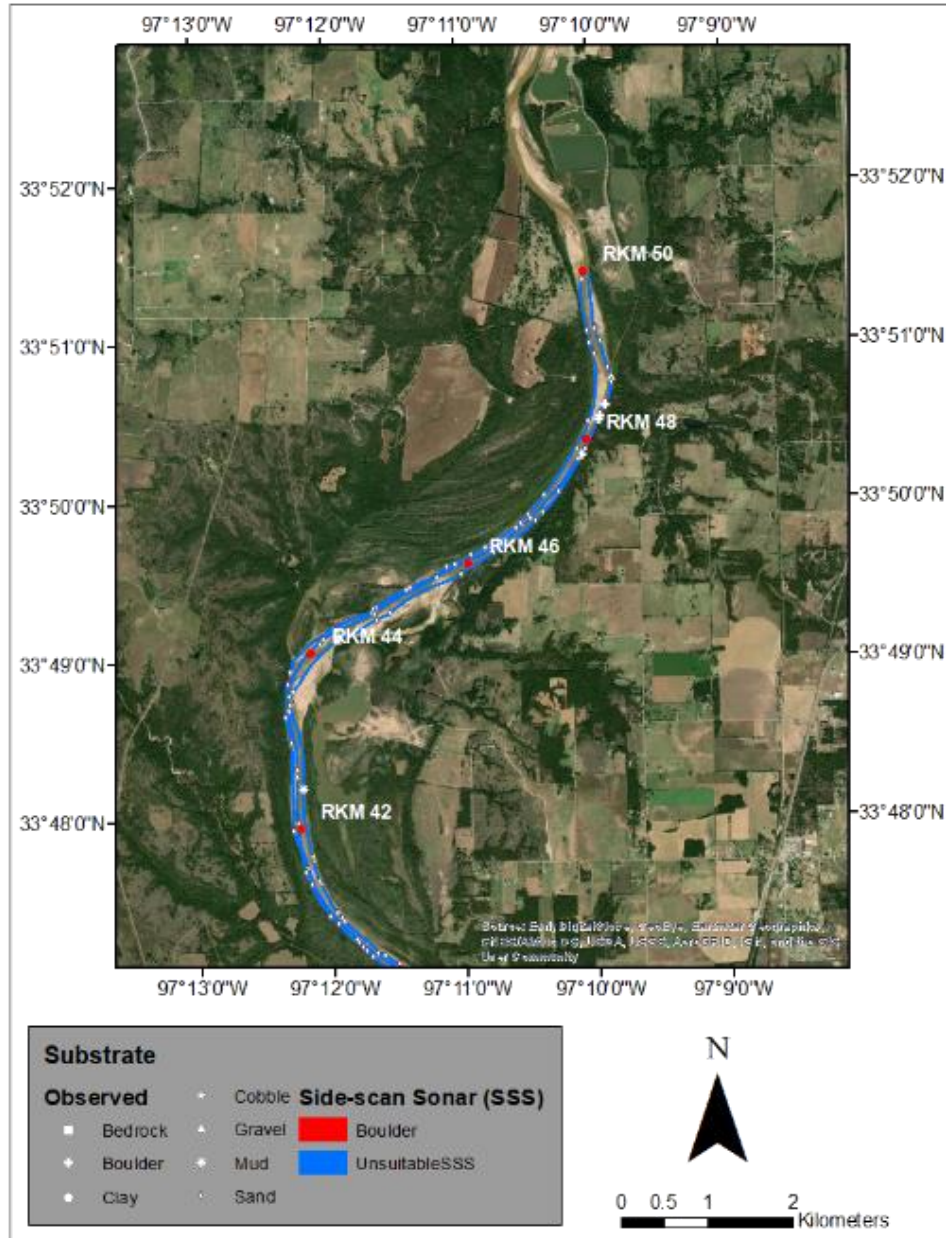


Figure 12.7 Substrate classification maps for the Red River overlaid on USDA aerial imagery. Substrates are classified by unsuitable or type of suitable substrate as determined by side-scan sonar. Symbols are given for ground truthing points according to the substrate that was found to be present at said point. Maps are listed from upstream to downstream according to river kilometers from the river-reservoir interface of Lake Texoma.

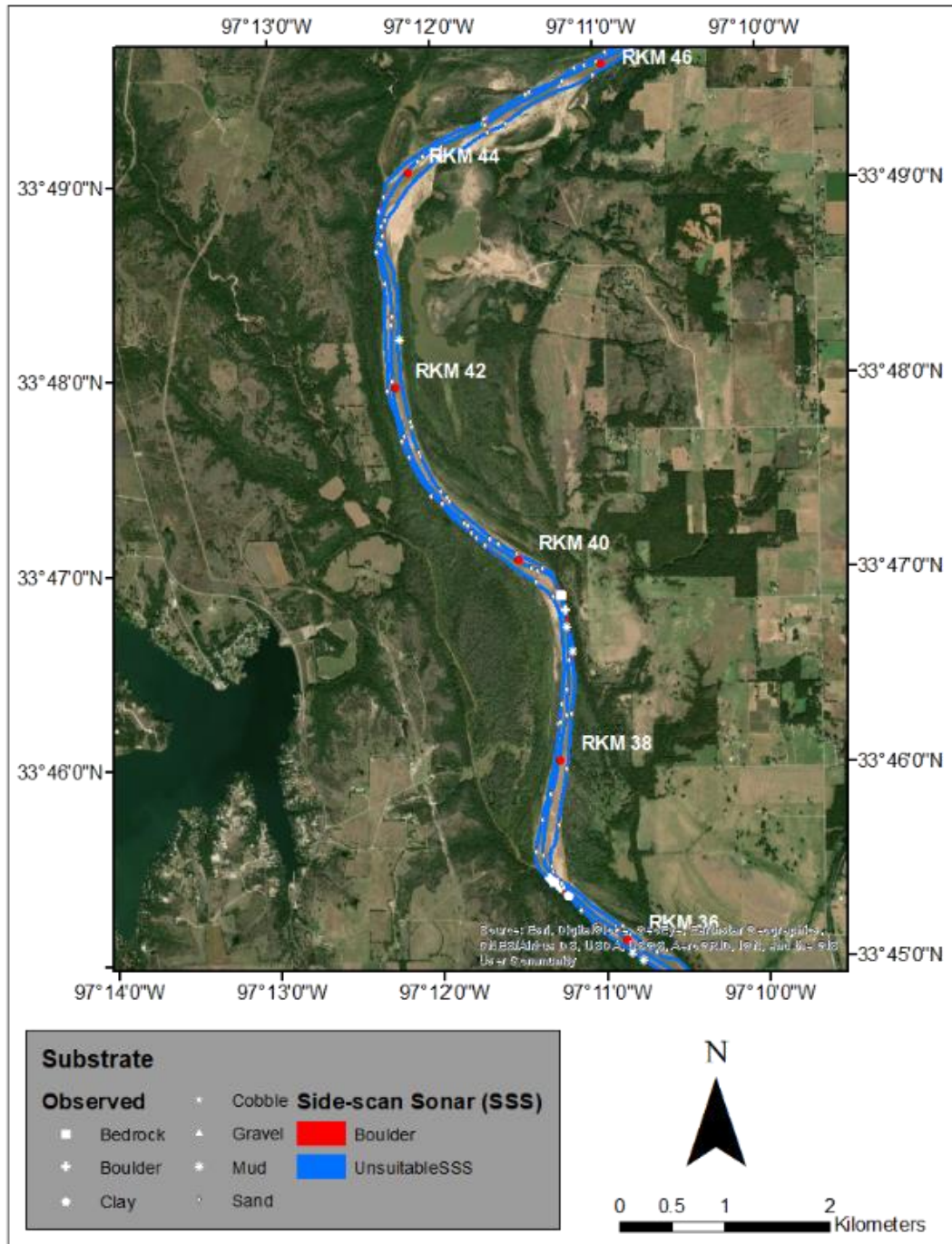


Figure 12.8

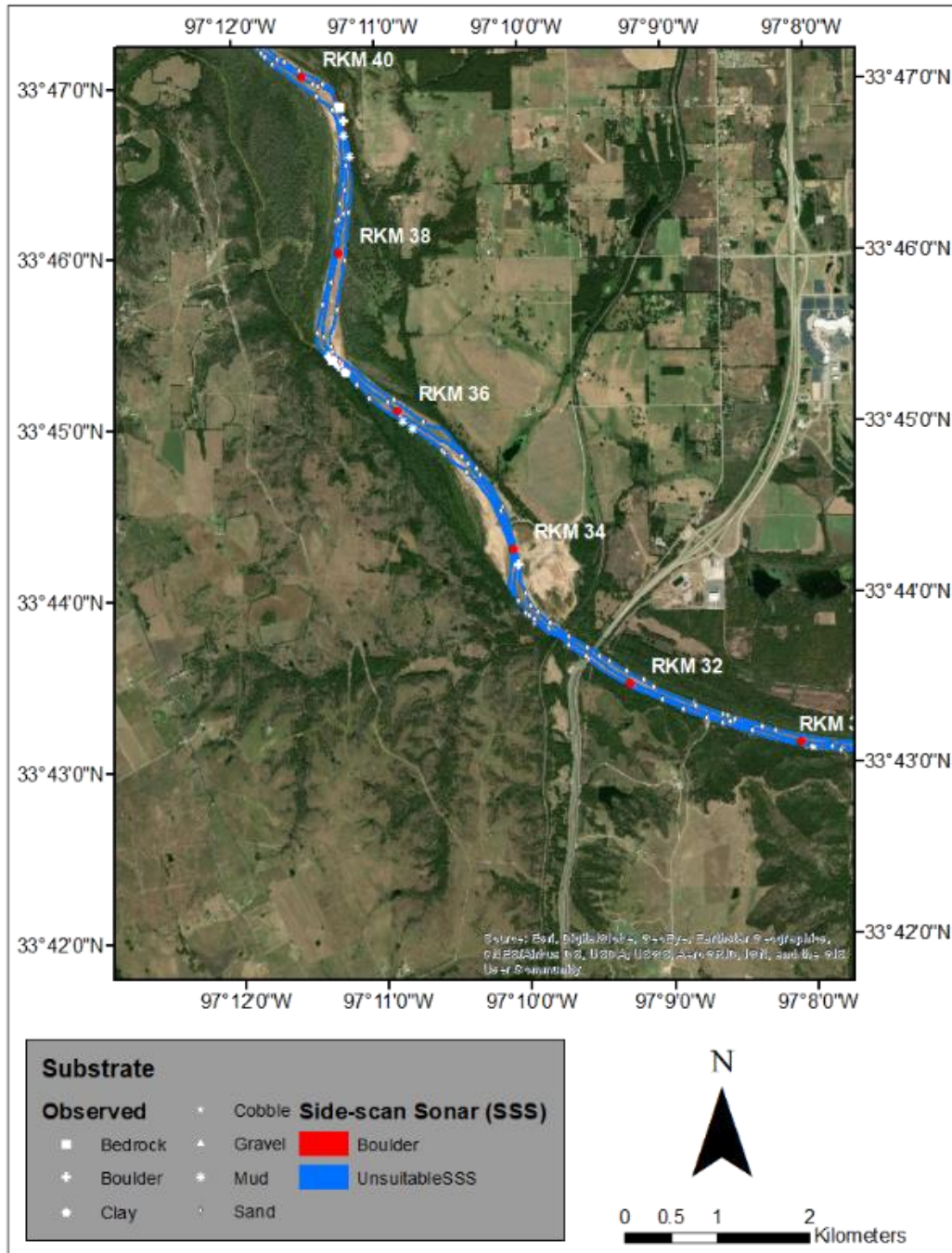


Figure 12.9

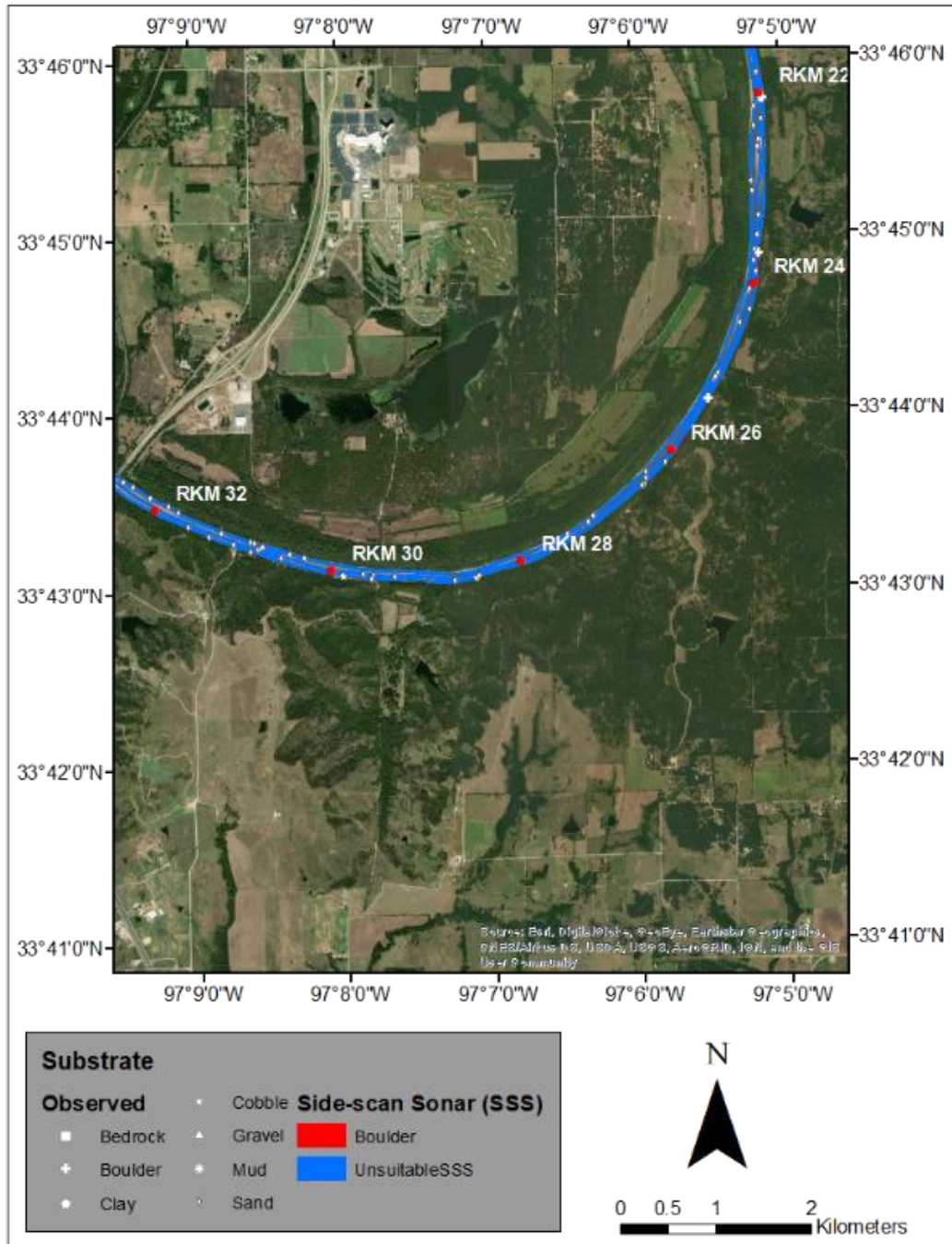


Figure 12.10

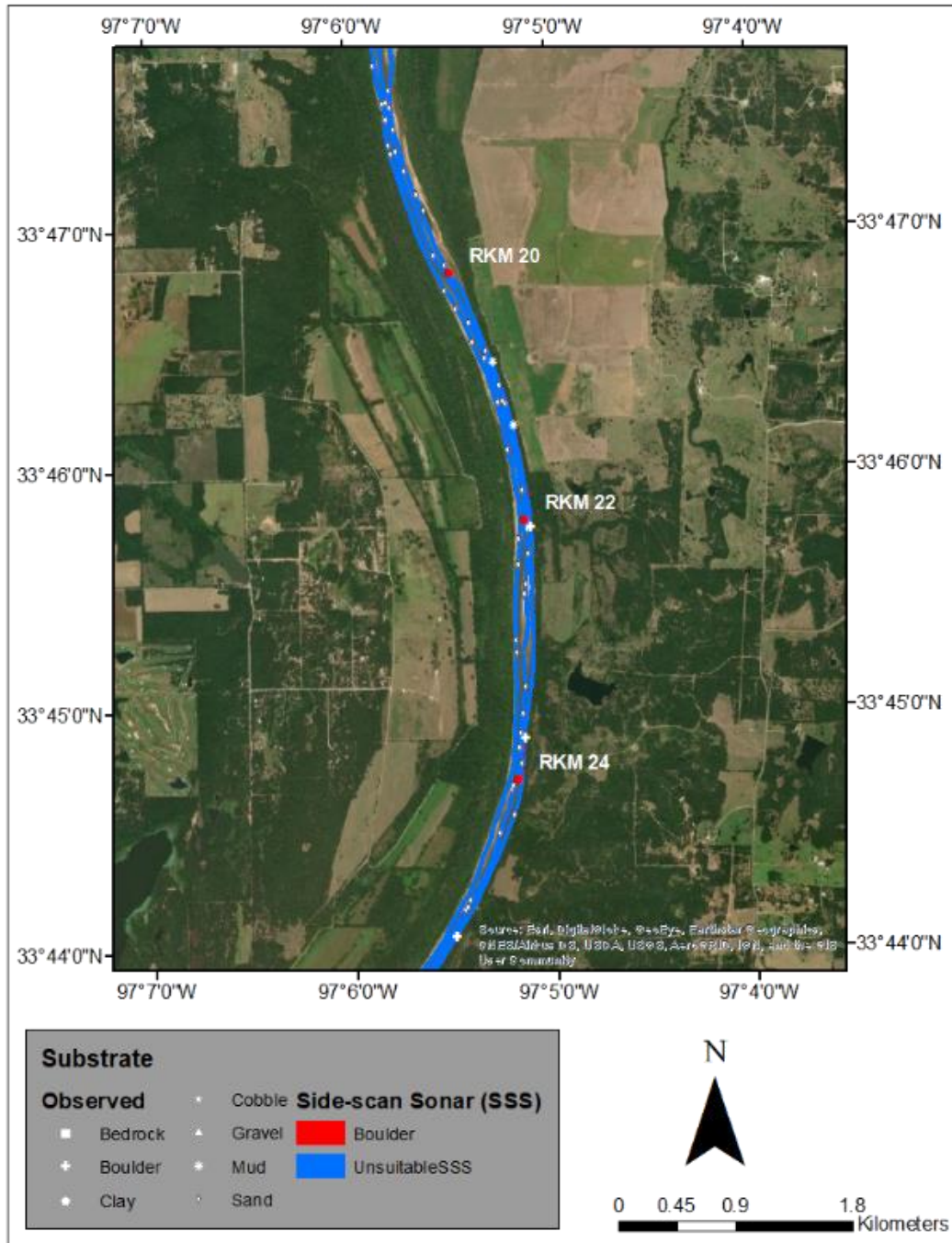


Figure 12.11

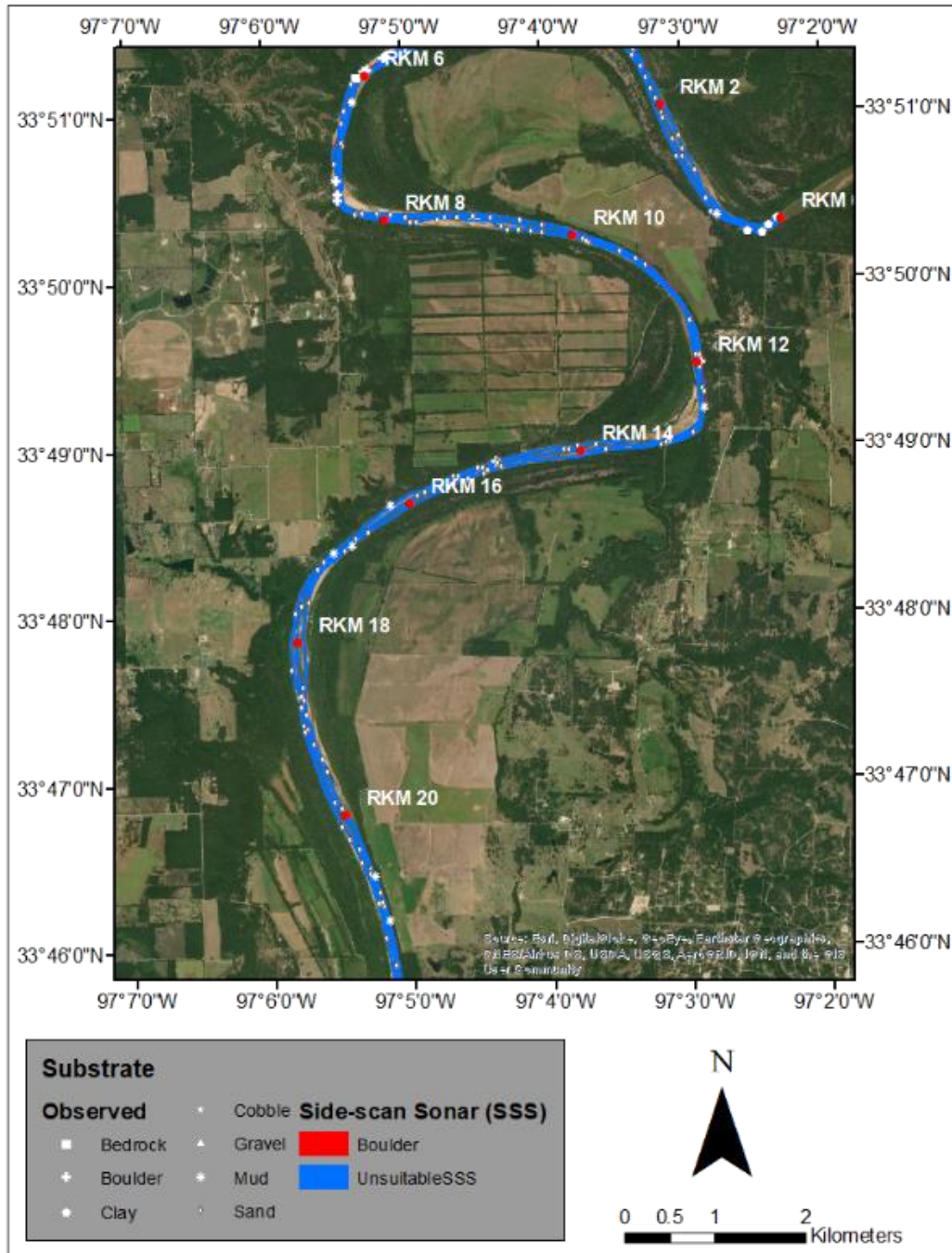


Figure 12.12

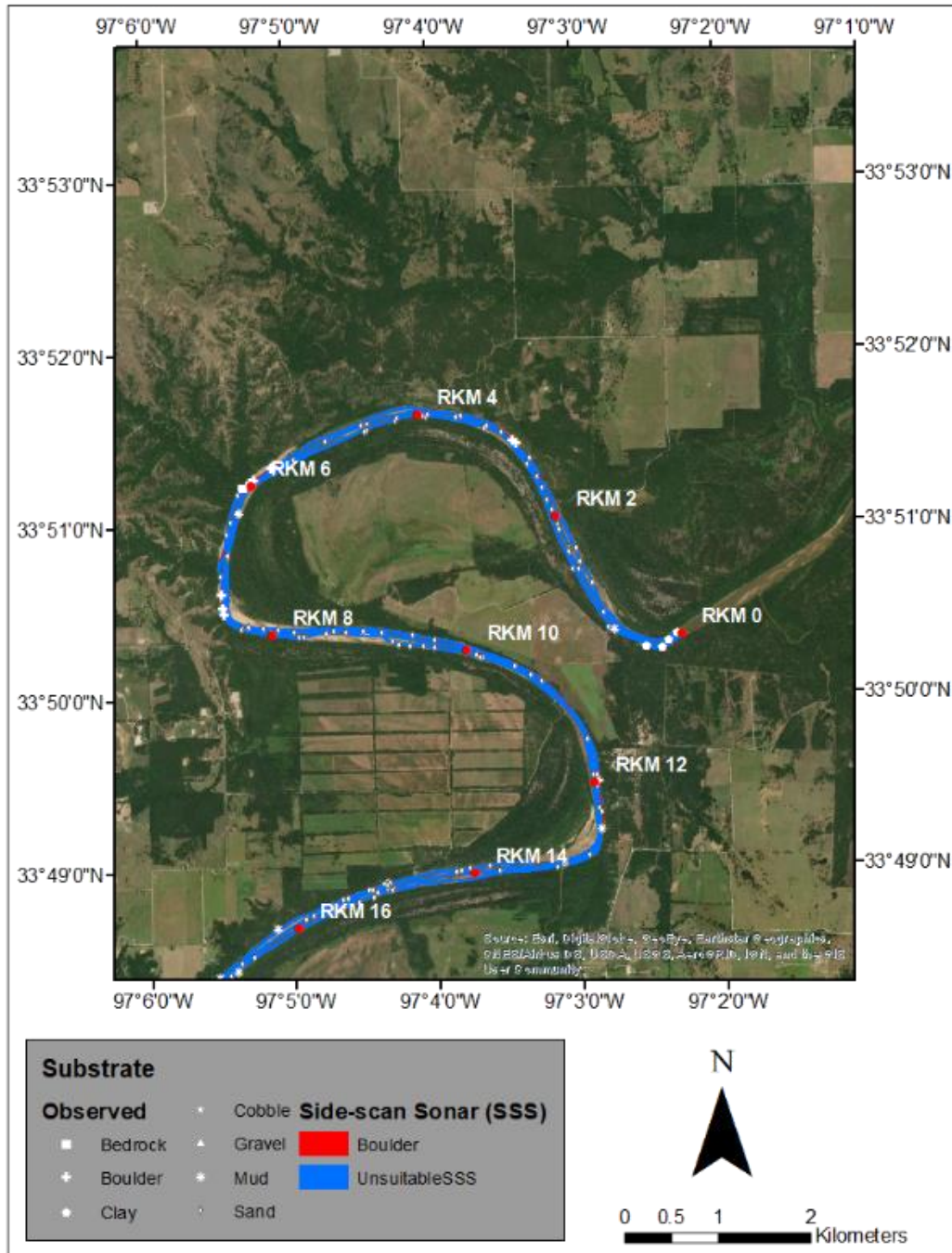


Figure 12.13

CHAPTER II

AVAILABILITY OF PADDLEFISH SPAWNING HABITAT IN OKLAHOMA RESERVOIR TRIBUTARIES AS A FUNCTION OF HYDROLOGY

ABSTRACT

American Paddlefish require discrete abiotic conditions such as water temperature, discharge, and substrate composition for successful spawning and recruitment during spring migrations. Population declines have prevailed throughout much of the species range because of anthropogenic habitat degradation altering the availability of these conditions. In Oklahoma, restoration stocking, as an attempt to mitigate local extirpation, has had variable success in reestablishing population in reservoirs throughout the state. Using maps of suitable substrate created from side-scan sonar imagery and digital elevation models (DEMs) from simultaneously recorded depth data, we analyzed the spatial and temporal availability of suitable substrate in seven reservoir tributaries during the spawning season. Substrate maps identified low proportions of suitable substrate (<1.5%) in all but one reservoir tributary, with narrow ranges of suitable substrate available throughout the spawning season. Reservoir tributaries associated with evidence of natural reproduction had generally higher spring discharges or larger proportions of suitable substrate than those without evidence. Suitable hydrology is likely an important driver of

successful spawning efforts, but other factors affecting the recruitment and survival of stocked Paddlefish may also be critical in the reestablishment of Paddlefish in reservoir systems.

INTRODUCTION

American Paddlefish *Polyodon spathula* is a potamodromous fish species that inhabits medium to large rivers in the Mississippi River drainage and surrounding Gulf Slope drainages (Jennings and Zigler 2000). In the spring, Paddlefish migrate upriver, coincident with increases in temperature and river discharge, to areas of gravel/cobble bars to spawn. However, anthropogenic riverine modification has degraded or destroyed spawning habitat in many areas for these fish, resulting in extirpation from portions their historic range (Unkenholtz 1986; Jennings and Zigler 2000). Dams are widely cited as the primary cause, blocking access to and causing the siltation of historic spawning grounds (Unkenholtz 1986). Even so, populations of Paddlefish have persisted in some impounded rivers, although the reasons for persistence are unknown.

In Oklahoma, where every major river has been impounded, Paddlefish have been limited to the lower portions of these systems, with few exceptions (Schooley and Neely 2016). To mitigate this reduction in range, Oklahoma Department of Wildlife and Conservation in conjunction with U.S. Fish and Wildlife Service have stocked Paddlefish in reservoirs where there are historical records of Paddlefish presence, in an effort to reestablish populations. Restoration efforts have been variable, though, and one factor hypothesized to affect success is the amount of suitable spawning substrates in reservoir tributaries.

Recently, four reservoirs that have had restoration efforts (Kaw, Oologah, Eufaula, Texoma) and one that has remained self-sustaining since impoundment (Keystone) were surveyed to quantify suitable substrates in reservoir tributaries (Chapter 1). Proportions of substrate varied among rivers with only the Verdigris River, the tributary of Oologah Lake, having proportions of suitable substrate greater than 40%. The remaining tributaries had small amounts of suitable substrate ($\leq 1\%$) with the large majority of tributaries being composed of sand or silt substrates. While the quantity of substrates has been thought to be a factor affecting restoration success, the Chapter 1 study only assessed substrate in a flat, 2-dimensional view. How the amount of suitable substrate might be affected by depth across variable hydrologic regimes is not clear and could be an additional factor contributing to successful spawning.

Hydrology correlates with Paddlefish reproduction (Miller et al 2008; Pracheil et al 2009; Miller et al 2011;), but few studies have investigated how hydrology and the availability of substrate affect recruitment of Paddlefish (Schooley and Neely 2016). Most recently, Schooley and Neely (2016) found that episodic recruitment in the Grand Lake system of Oklahoma-Kansas was linked to years of sustained high discharge events during the spawning season. Significantly, Schooley and Neely (2016) concluded that recruitment was tied to availability of suitable spawning substrate as a function of flow variation in upstream tributaries. Recent advances in remote sensing and spatial analyses have made modeling this type of relationship less costly and time consuming (Kaeser and Litts 2011; Schooley and Neely 2016). Using sonar to create habitat maps along with associated depth data allows for rapid modeling of a river's relationship between hydrology and explicit habitat types. Depth data collected from sonar surveys can be used to describe a rivers bathymetry using spatial extensions in GIS software to create DEMs (Digital Elevation Models). Describing this relationship would allow for a more refined analysis of how availability of suitable substrate abundance may affect Paddlefish population stability beyond the flat, 2-dimensional environment. For this project, we used estimates of suitable substrate availability from Chapter 1 to conduct research into the role of water depth as it varies daily and annually with hydrology to investigate how depth and substrate interact with hydrology to effect Paddlefish population sustainability in seven reservoir tributaries throughout the state of Oklahoma.

METHODS

Study Area

The focus of this research was five river-reservoir systems in the Arkansas River and Red River drainages of Oklahoma (Figure 1; Table 1 and 2) where Paddlefish persist or have been stocked (Table 3). These river-reservoir systems differ in size, location, and amount of suitable spawning substrate for Paddlefish.

Kaw Lake, Arkansas River — Kaw Lake is the most upstream reservoir on the Arkansas River in Oklahoma and is managed as a hydropower facility. Throughout the early to mid-1990's, Kaw Lake was stocked with 48,000 Paddlefish and evidence of natural reproduction was found in 2017 with state biologists confirming multiple reports of anglers catching juvenile Paddlefish in cast nets (J. Schooley, ODWC, personal communication). A lowhead dam on the Arkansas River, approximately 129 km upstream, exists near Wichita, KS and likely limits upstream migration of Paddlefish except during extreme high flows (Neely et al. 2015; Pennock et al. 2018). The Arkansas River above Kaw Lake had an estimated 2.62 ha of suitable substrates composed mostly of boulder and some cobble (Chapter 1, Tables 4 and 5).

Keystone Lake, Arkansas and Cimarron rivers — Keystone Lake is located downstream of Kaw Lake, at the confluence of the Arkansas and Cimarron rivers in northcentral Oklahoma. The lake has no history of being stocked with Paddlefish, but has a self-sustaining population that supports recreational harvest and holds the current state and world records (ODWC 2021). The Cimarron River is a largely unimpeded prairie river that flows east from its origins in New Mexico, and has large variations in flow dependent on precipitation. Furthermore, the Cimarron River has high concentrations of dissolved and suspended sediments, and has a dominant substrate of sand (Reash 1990; Paukert and Fisher 2001). These findings were confirmed by

substrate surveys in 2020, which found only 3.6 ha of suitable substrates, mainly boulder, with the remaining being mostly unsuitable sand (Chapter 1). The Arkansas River flowing into Keystone Lake is regulated by discharge from upstream Kaw Dam, with a mean annual discharge of 175.2 cms and is the largest river under study. The Arkansas River in this stretch is a wide and shallow braided prairie river, substrate surveys found this section was dominated by sand substrates with only 5.2 ha of suitable substrates identified (Chapter 1, Tables 4 and 5).

Eufaula Lake, North Canadian River — Lake Eufaula is the second largest reservoir in Oklahoma by water volume, and the largest by surface area at 42,690-ha. The lake was created by damming the Canadian River just before its confluence with the Arkansas River, and is near the town of Eufaula in eastern Oklahoma. Over 200,000 Paddlefish were stocked in Lake Eufaula between 2007 and 2017 and a small-scale snag fishery was evident by 2015 (Jager and Schooley 2016). On the northern end of the lake, the North Canadian River flows from the west with a mean annual discharge of 26.0 cms. The North Canadian River is illustrative of typical prairie rivers, being shallow and braided. Substrate surveys identified only 4 ha of boulder substrates with the majority of the river being comprised of sand or mud (Chapter 1, Tables 4 and 5). On the southern end of the lake, the Canadian River (also known as South Canadian River) is the contributing tributary but was not surveyed by sonar because of hydrological and morphological limitations, but remote sensing from aerial imagery failed to find any suitable substrates for spawning by Paddlefish (Chapter 1).

Oologah Lake, Verdigris River — Oologah Lake was created by damming the Verdigris River just east of Oologah, Oklahoma. Stocking of over 30,000 Paddlefish occurred from 1995-2000 and data acquired from the ODWC Paddlefish Research Center and ODWC e-check harvest indicate that over 100 fish have been harvested from the Verdigris River and its

tributaries since 2014 (J. Schooley unpublished data). Paddlefish population monitoring surveys were conducted by ODWC in 2013 and 2014, of which 99.7% of fish collected did not have coded wire tags, indicating they were the product of natural reproduction (J. Schooley unpublished data). The Verdigris River is a deep, channelized river with well-defined and high stable banks, and the riverbed is comprised of rock, shale and bedrock substrate (Wallen 1956). Substrate surveys found 158.2 ha of suitable substrates, with substrate types consisting of gravel/cobble, boulder, and bedrock. The dominant substrate class was gravel/cobble, which represented 37% of the total area surveyed. The remaining 54% of area was classified as unsuitable, consisting of mud, clay or silt (Chapter 1, Tables 4 and 5). Just above the confluence with Oologah Lake, the Verdigris River has a mean annual discharge of 85.7 cms and is the second largest river under study. The Verdigris River is free-flowing for approximately 245 river km from Toronto Lake near Toronto, Kansas to Oologah Lake and is characterized by a series of wide bends connected by straight segments (Wallen 1956).

Lake Texoma, Red and Washita rivers — Lake Texoma is the largest lake in Oklahoma by water volume, and was created by impounding its two tributaries, the Red and Washita rivers. Stocking occurred from 1999 to 2007, although no natural reproduction was ever reported and high annual mortality was evident (Patterson 2009). Despite this, in 2015 there were reported catches of Paddlefish in the Red River, including Lake Texoma (Jager and Schooley 2016). The Red River flows across the modern Oklahoma-Texas border, and is shallow, braided and wide with substrate surveys finding only 4.74 ha of boulder substrates and majority of the river being composed of sand or mud (Chapter 1, Tables 4 and 5). The mean annual discharge of the Red River is 89.5 cms but is highly variable throughout the season. The Washita River originates in the Texas panhandle and, in the 50-km segment above the lake, is channelized with steep banks

and the dominant substrates of mud and sand. (Matthews 1988; Patterson 2009). Throughout substrate surveys in the Washita River, only 1.2 ha of suitable habitat, which consisted of cobble and boulder, were identified (Chapter 1, Tables 4 and 5).

Side-scan Sonar Substrate Mapping

Side-scan Sonar Data Collection –We mapped 7 reservoir tributaries using a Humminbird MEGA SI sonar unit using two to three downstream passes depending on river width (Figure 1.) Transects were established with beginning and end points to standardize sections of river and depth points were recorded every 0.8 meters along with SSS imagery. Data were collected during high discharge events at the 80th percentile of mean daily flow or higher on a 50 km stretch of river above the river-reservoir interface to quantify substrate available to Paddlefish during spawning.

Side-scan Sonar Imagery Analysis – SSS imagery was imported into ReefMaster 2.0 software to blend, enhance and analyze data from SSS transects. Transects from the same river were merged in ReefMaster 2.0 using the mosaic tool to create one contiguous image of SSS data and substrate identified by particle size (i.e., silt/sand, gravel, cobble, boulder, bedrock; Wentworth 1922) was classified based on the image texture, tone, shape and pattern from the SSS imagery (Kaesler and Litts 2010; Figure 2). Substrates identified as gravel, cobble, boulder and bedrock were all considered suitable, others were considered unsuitable. Polygons were constructed around substrate types in Reefmaster 2.0, exported to ArcMap 10.8, and summarized by area (ha). Additional details for classifying substrate types from SSS imagery are found in Chapter 1.

Hydrology and Digital Elevation Models

Stage Discharge Model – Predictive models were first created to explain the relationship between river discharge and gage height in our seven study rivers using two or three polynomials (Table 6).

Two polynomial predictive model: Stage = $a_1(\text{CMS})^2 + b_1(\text{CMS}) + c_1$

Three polynomial predictive model: Stage = $a_1(\text{CMS})^3 + b_1(\text{CMS})^2 + c_1(\text{CMS}) + d_1$

We compiled 15-minute discharge and gage height data from USGS gages during the spawning season (March – May) from years when SSS surveys were conducted (Table 7). Data points above the highest discharge level surveyed for each river were excluded from these models to reduce influence of flood conditions from normal springtime discharge on predictive models. Using these models, we predicted gage height at the lowest river discharge surveyed, the lowest discharge recorded for that time period, and four points of discharge evenly distributed between the two (Table 7) to create depth points of reference for the creation of triangulated irregular networks (TIN) as a digital elevation model.

Triangulated Irregular Network Creation – A triangulated irregular network (TIN) is a form of digital elevation model that creates a representation of a continuous surface consisting of triangular facets constructed from a group of points with elevation values. Bathymetric TINs of our study rivers were created using depth points collected during SSS transects and manually-located points of the bank (0-depth) identified in SSS imagery (Figure 3). Depth points collected during SSS transects were uploaded to ReefMaster 2.0 in conjunction with SSS imagery and then exported to ArcMap 10.8 as 3D point shapefiles with latitude and longitude (x and y coordinates) as well as depth values (z coordinates) in negative meters. In rivers where bank-to-bank coverage by SSS was collected, both riverbanks were outlined by individual points spaced approximately 2.5 m apart (Figure 4). Rivers where bank-to-bank coverage was not available, because of large river widths or shallow river environments, only the bank closest in distance to areas of identified suitable substrate was outlined (Figure 4). Additionally, because of the scarcity of suitable substrates in some rivers, TINs were only created in areas where suitable substrates were identified because the change in availability of unsuitable substrates with discharge was not of interest.

Creation of TIN's for each river was separated into sections determined by sampling date to account for the different hydrological conditions that occurred over the multiday sampling period. Using original depth values of points collected from SSS transects and points outlining banks, the Create TIN tool was used in each section, creating a separate TIN for each sampling day. Following TIN creation, the Delineate TIN tool was used with a maximum distance between points of 100 to remove sections of TIN interpolated outside of areas where suitable substrates were identified.

Identification of Substrate Availability at Flow – Using the six predicted gage heights from our Stage ~ Discharge models, we created contour lines inside each river's TIN to obtain total area of suitable substrate available at each height (Table 6). Models were constricted by the lowest level of discharge during SSS surveys and the minimum discharge recorded during spring of surveyed years (Table 7). Sections of TIN that were surveyed at discharges greater than the lowest discharge day were adjusted to this level using the difference in gage heights as predicted by our Stage ~ Discharge Models. As such, the section of TIN surveyed on the day with the lowest discharge only had 5 contour lines because substrate surveyed on that day was the maximum area surveyed, whereas the remaining sections of TIN had 6 contour lines with the additional contour line adjusting the TIN to the section of river surveyed during lowest discharge.

Adjusted contour lines created for each TIN section were merged, connected, and then transformed into polygons. In cases where bank-to-bank coverage was possible, contours were connected at the beginning or end of each area of identified suitable substrate. However, in cases where bank-to-bank coverage was not possible, contour lines were linked to the beginning and end of depth points of each area with identified suitable substrate (Figure 4). From these methods, the amount of suitable substrate was estimated inside each contour polygon for creating models of the amount of suitable substrate area in relation to river stage and discharge.

Substrate Discharge Model – Predictive models of area of suitable substrate at discharge using the information from the stage-discharge relationship were subsequently created with either two or three polynomials to maximize predictive performance:

Two polynomial predictive model: $\text{Substrate} = a_2(\text{CMS})^2 + b_2(\text{CMS}) + c_2$

Three polynomial predictive model: $\text{Substrate} = a_2(\text{CMS})^3 + b_2(\text{CMS})^2 + c_2(\text{CMS}) + d_2$

These models were then applied to daily discharge values across the spawning season (March – May) from 2011 to 2020 acquired from each river’s respective USGS gage station to summarize substrate availability among years in our study rivers. Spring spawning discharges were summarized by mean yearly discharge, mean yearly days above 80th percentile and mean yearly consecutive days above the 80th percentile to describe how a rivers hydrology might affect Paddlefish reproduction. Although the threshold of discharge needed to support the entirety of Paddlefish reproductive efforts may vary among rivers, the 80th percentile was chosen to standardize representative high discharge events among rivers.

RESULTS

Across all river systems, we classified substrates in 2,700.4 ha of river with varying proportions of suitable and unsuitable substrates (Chapter 1; Table 4). Among rivers surveyed, only the Verdigris River had proportional suitable substrate areas exceeding 40%; the remaining rivers had minimal (<1.5%) amounts of usually large suitable spawning substrate in the study reach, mostly being comprised of unsuitable sand or mud (Table 4 and 5).

The predictive models for our study rivers encompassed similar ranges of discharges among rivers and had high R^2 values (Tables 6 and 7). All Stage ~ Discharge models used three polynomials and all Habitat ~ Discharge models used two polynomials with the exception of the Verdigris River Models where the inverse was true (Table 6). Ranges of discharges used to construct the models ranged from the 31st to the 59th percentile at the lower end among rivers and exceeded the 90th percentile at the upper end (Table 7).

Spring discharges statistics varied among rivers and years, and, in general, rivers with larger discharges were associated with systems with evidence of natural reproduction (Tables 9-12; Figures 6-13). The Arkansas River above Keystone and the Verdigris River had the highest mean spring discharges across the entire study period as well as interannually among study rivers, whereas the North Canadian and Cimarron rivers had the lowest mean spring discharge (Tables 9 and 10). Additionally, rivers associated with natural reproduction generally had higher mean discharges in the spring spawning season compared to the entire water year. Rivers not associated with evidence of natural reproduction tended to have higher number of mean days above the 80th percentile of flow across the study period, but differences were small and the range of mean days above the 80th percentile across all rivers ranged from 20.3 to 30.2 (Table 12).

The range of available suitable substrates between the minimum and maximum discharge in our models was generally low among study rivers (Table 5, Figure 12). In particular, the Cimarron, North Canadian and Washita rivers all had a range of less than one hectare of suitable substrate (Figure 5). The

difference in the proportion of suitable substrates across the modeled range was only > 0.5 in the Arkansas River above Keystone and the Verdigris and Red rivers. Additionally, the Verdigris River had the largest variation in substrate availability (130.5 – 157.9 ha), and the largest range in modeled percentiles of flows (Table 5). This indicates that even during low discharge events, the Verdigris River still had a much higher proportion of suitable substrates than any other river under study.

DISCUSSION

Depth data from sonar surveys can be easily applied to analyze river bathymetric habitat data and gain additional insight into how hydrology affects habitat availability. As it applies to Paddlefish, these data provide an essential picture of the historical spawning potential of a long-lived species that may spawn infrequently based on abiotic conditions (Jennings and Zigler 2000).

In general, we found that rivers with larger proportions of suitable spawning substrates or higher spring spawning hydrologic statistics coincided with systems with natural reproduction. The Verdigris River fits both categories, with the highest proportion of suitable spawning substrates as well as the second highest spring discharge among rivers. Additionally, the Verdigris River had the highest difference between mean annual discharge and spring spawning season mean discharge, $24.8 \text{ m}^3/\text{s}$, providing increased discharge events when Paddlefish would benefit most. The Arkansas River above Keystone Lake has the highest spring discharge under study and supports a robust recreational Paddlefish fishery, despite low abundance of suitable spawning substrates in the study area. Additionally, Kaw Lake exhibited high discharge years when recruitment has been observed. This could also be a result of the Walnut River, a tributary of the Arkansas River above Kaw, where large proportions of suitable substrate were present (Chapter 1) indicating it may be a source of spawning instead of the Arkansas River itself (Neely et al. 2015).

In the Arkansas River above Kaw and the Arkansas River above Keystone, where availability of suitable substrate is low, years of consecutive days of high discharge in the spring may mitigate the effects of low proportion of suitable substrates. One of the few documented recruitment events in the Arkansas River above Kaw Lake was in 2017 when the river had its highest number of days above the 80th percentile in the spring and the most consecutive days above the 80th percentile among any study year or river. Although the Arkansas River above Keystone had the second highest amount of suitable substrate, the difference among most rivers under study was not large ($< 4 \text{ ha}$). Being the largest river under study, the high spring discharges could be responsible for successful recruitment despite the lack of

large proportions of suitable substrates. Additionally, we only surveyed 50 km of each of our study rivers, and Paddlefish migrate hundreds of kilometers (Jennings and Zigler 2000; Paukert and Fisher 2001), areas of suitable spawning substrate could exist outside of the surveyed areas that could be used by Paddlefish.

When comparing suitable substrate availability and spring hydrology of study rivers, similarities suggest minimal potential for natural reproduction. The Cimarron and North Canadian rivers, for example, had similar spring discharge statistics and suitable substrate availability, both having low spring discharge statistics and low amounts of available spawning substrate. In the Keystone Lake system, evidence suggest that the majority of Paddlefish use the Arkansas River over the Cimarron River for their spawning migration and (Paukert 2001) and our data would suggest that low availability of suitable spawning substrates coupled with low spring discharge contributes to that difference. As a result, we would hypothesis low reproductive potential of the North Canadian River for Paddlefish stocked in Lake Eufaula. Conversely, the Washita and Red rivers of Lake Texoma, where no evidence of Paddlefish reproduction exists, show similarities to the Arkansas River above Kaw, where natural reproduction has occurred. However, the best evidence suggests that reproduction above Kaw Lake was limited to only one year out of the ten we studied. Whether reproduction in the Lake Texoma system is occurring or is limited to only a few suitable years is unknown. Moreover, differences other than hydrology and availability of suitable spawning substrates, such as predation pressure (Patterson 2009), may be more important.

A suite of other factors, such as genetics, predation and foraging ability may also be important in maintaining self-sustaining Paddlefish populations (Paukert 2001; Parken and Scarnecchia 2002; Mero et al. 2011, Eachus 2021). Successful restoration in reservoirs hinges not only on the survival of stocked fish to sexual maturity, but subsequent spawning by the stocked population and survival of resultant progeny to adulthood. Paddlefish stocked in Lake Texoma were of Grand Lake origin, which differ genetically from the Red River population that historically occupied the region (Schwemm et al. 2015). Fish stocked from outside sources have genetics that are less fit for their new environment (Ward 2006), which could have affected survival or spawning ability in Lake Texoma, where extremes in temperature and salinity

are prevalent. Additionally, mortality of stocked Paddlefish is also affected by the abundance of large predators (Parken and Scarnecchia 2002; Mero et al 2011). In Lake Texoma, where there is an abundance of Striped Bass (*Morone saxatilis*), and predation of stocked Paddlefish was considered a potential contribution to the failure of restoration efforts there (Patterson 2009). Moreover, larval Paddlefish are visual zooplanktivores and may be negatively affected by high reservoir tributary turbidity. High turbidities in rearing habitat of reservoir tributaries like the Washita and Red rivers could lead to decreased success in foraging and poor recruitment (Eachus 2021).

Future research is needed to improve our understanding of the influence of multiple factors on Paddlefish reproductive success. A microchemistry analysis of Paddlefish dentaries in the Keystone Lake system would provide an understanding of the contribution of each reservoir tributary to the population, allowing for inference about the importance of hydrologic differences between the Cimarron and Arkansas Rivers. Additionally, research focused on the abiotic and biotic foraging needs of larval Paddlefish may help explain why rivers similar in composition of suitable substrates and spring hydrology do not support natural reproduction.

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TABLES AND FIGURES

Table 1. Physical size characteristics of reservoirs in Oklahoma where estimates of suitable spawning substrate quantity for Paddlefish were acquired in connected tributaries. Measurements are based on water elevations in the reservoir at conservation pool level.

Reservoir	Volume (m ³ x 10 ⁶)	Surface Area (ha)	Max Depth (m)	Year Impounded
Kaw	447.1	6,895	22.7	1976
Keystone	532.8	9,554	22.3	1968
Oologah	563.9	11,920	21.9	1963
Eufaula	2,707.3	42,690	27.5	1964
Texoma	3,022.5	36,000	43.3	1944

Table 2. Hydrologic characteristics of tributary rivers to Oklahoma reservoirs where surveys of potentially suitable spawning substrate for Paddlefish were carried out in 2019-2021. Discharge values were calculated using 2011 – 2020 water years from the respective USGS gage.

River	USGS Gage	Mean Annual Discharge (m ³ /s)	Median Discharge (m ³ /s)	80 th Percentile (m ³ /s)	Variability ¹	Watershed Area (km ²)
Arkansas Above Kaw	07146500	64.2	25.3	65.83	3.73	113,216
Arkansas Above Keystone	07152500	175.5	71.9	239.02	3.47	141,063
Cimarron	07161450	38.5	12.7	31.58	4.20	46,565
North Canadian	07242000	26.0	9.9	27.76	1.71	37,010
Verdigris	07171000	85.7	15.5	124.52	2.28	9,424
Washita	07331000	51.4	17.2	63.96	2.64	18,653
Red	07316000	89.5	19.7	90.56	3.07	79,725

¹Variability across annual flows calculated by subtracting the 10th percentile from the 90th

Table 3. Stocking history of Paddlefish into six reservoirs in Oklahoma provided by Tishomingo National Fish Hatchery.

Reservoir	# Stocked	Stocking Years	Confirmed Natural Reproduction
Keystone	0	N/A	Yes
Kaw	48,000	1991-1995	Yes
Oologah	30,458	1995-2000	Yes
Eufaula	200,423	2007-2017	No
Texoma	119,520	1999-2007	No

Table 4. The total amount of suitable and unsuitable substrates found during SSS surveys for each reservoir tributary surveyed and the respective status of natural reproduction from their reservoirs.

Reservoir	Status	River	Suitable (ha)	Unsuitable (ha)
Kaw	Natural Reproduction	Arkansas River	2.62	395.7
Keystone	Natural Reproduction	Arkansas River	5.2	571.2
		Cimarron River	3.6	350.5
Eufaula	No evidence	North Canadian	4.0	274.7
Oologah	Natural Reproduction	Verdigris	158.2	186.9
Texoma	No Evidence	Washita	1.2	242.1
		Red	4.74	499.7

Table 5. Percentage of presumably suitable (gravel/cobble, boulder and bedrock) and unsuitable (silt/sand/mud) substrate for Paddlefish in the 50-km of river upstream of the river-reservoir interface surveyed by side-scan sonar.

Rivers	Unsuitable %	Suitable %		
		Gravel/Cobble %	Boulder %	Bedrock %
Arkansas Kaw	99.3	<0.1	0.6	0
Arkansas Keystone	99	0	<1	<0.1
Cimarron	99	0	1	0
North Canadian	98.5	0	1.5	0
Verdigris	54	37	6.25	2.75
Washita	99	<0.1	<1	0
Red	99	0	1	0

Table 6. Parameters and R^2 values associated with each rivers Stage ~ Discharge or Substrate ~ Discharge models used to quantify suitable substrates throughout the spawning season from 2011 – 2020.

Parameter	Arkansas Kaw	Arkansas Keystone	Cimarron	North Canadian	Verdigris	Washita	Red
<u>Stage ~ Discharge Model</u>							
a_1	-0.000000506	0.00000005366	0.0000004033	0.000001245	-0.000004958	-0.00002601	0.0000005345
b_1	-0.00003287	-0.00000743	-0.0001455	-0.0002733	0.01121	0.01382	-0.00004527
c_1	0.01125	0.005501	0.02443	0.02922	1.36	2.305	0.01581
d_1	0.9992	1.156	1.925	1.595			2.176
R^2	0.9972	0.9965	0.9973	0.9963	0.9999	0.9989	0.9976
<u>Substrate ~ Discharge Model</u>							
a_2	-0.000005778	-0.00001018	-0.0001532	-0.0003087	0.0000006	-0.000002569	-0.00006142
b_2	0.008627	0.1201	-0.000234	0.03609	-0.000622	0.002157	0.02624
c_2	0.3458	1.394	3.607	2.902	0.2213	0.8401	1.572
d_2					130.4		
R^2	0.9971	0.9967	0.997	0.9984	0.9973	0.9968	0.9968

Table 7. Associated hydrology for rivers surveyed by side-scan sonar used for model creation. Discharge threshold is the lowest recorded discharge during side-scan sonar surveys, whereas low discharge is the lowest recorded discharge during the spawning season during surveyed years by a river’s respective USGS gage. Percentile range is the percentile of the minimum and maximum discharge values calculated using daily flow values from each river’s respective USGS gage from 2011 – 2020. Substrate range is the amount of suitable substrate available from the minimum discharge to the maximum discharge.

River	Surveyed Years	Percentile Range	Substrate Range (ha)	Minimum Discharge (m ³ /s)	Maximum Discharge (m ³ /s)
Arkansas Kaw	2021	54 th – 93 rd	0.5 – 1.64	17	169.9
Arkansas Keystone	2019 - 2020	31 st – 92 nd	1.8 – 4.79	31	481
Cimarron	2019 – 2020	59 th – 91 st	2.8 – 3.57	16.4	70.8
North Canadian	2019 – 2020	57 th – 91 st	3.3 – 3.96	12.62	56.6
Verdigris	2019	48 th – 96 th	130.5 – 157.9	13.98	424.5
Washita	2020	52 nd – 93 rd	0.89 – 1.16	18.4	169.8
Red	2020	46 th – 90 th	2.16 – 4.35	22.36	198.1

Table 8. Gage height (GH, meters) values for contour lines as predicted from rivers Stage ~ Discharge models. Point 1 represents the lowest discharge and point 6 represents the highest with points in between being evenly distributed. Discharge from points 1 and 6 were drawn from minimum and maximum discharge values for each river.

River	Arkansas Kaw		Arkansas Keystone		Cimarron		North Canadian		Verdigris		Washita		Red	
	GH	(m ³ /s)	GH	(m ³ /s)	GH	(m ³ /s)	GH	(m ³ /s)	GH	(m ³ /s)	GH	(m ³ /s)	GH	(m ³ /s)
Point 1	1.18	17	1.32	31	2.29	16.4	1.92	12.62	1.51	13.98	2.55	18.39	2.51	22.36
Point 2	1.47	47.58	1.72	121	2.49	27.3	2.11	21.42	2.39	96.1	2.92	48.67	2.95	57.51
Point 3	1.7	78.16	2.04	211	2.67	38.1	2.26	30.2	3.21	178.2	3.23	78.95	3.29	92.66
Point 4	1.9	108.74	2.28	301	2.81	48.9	2.39	39	3.95	260.4	3.5	109.23	3.57	127.8
Point 5	2.07	139.32	2.49	391	2.95	59.7	2.5	47.8	4.6	342.4	3.73	139.51	3.78	162.95
Point 6	2.21	169.9	2.68	481	3.07	70.8	2.6	56.6	5.23	424.5	3.9	169.8	3.95	198.1

Table 9. Mean daily discharge (m³/s) during March to May from 2011 to 2020 for each river under study.

River	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020
Arkansas Kaw ¹	19.85	36.19	21.75	19.4	48.34	53.53	111.99	20.09	100.71	70.7
Arkansas Keystone ¹	47.22	198.47	59.13	37.96	130.55	174.14	296.57	57.12	284.69	284.86
Cimarron ¹	12.58	28.56	20.72	6.92	28.44	26.64	43.54	8.76	52.17	30.09
North Canadian	16.03	16.89	23.96	12.92	30.04	25.27	27.36	19.61	40.47	39.09
Verdigris ¹	63.94	113.6	65.98	26.14	107.54	100.1	164.79	39.67	201.87	221.45
Washita	23.36	47.76	33.24	18.6	61.1	77.89	66.37	57.34	113.89	98.21
Red	24.56	43.47	24.09	22.36	75.13	103.3	92.52	53.92	162.07	101.43

¹Indicates a river system associated with a reservoir with wild recruitment of Paddlefish

Table 10. Days above the 80th percentile of flow from March to May recorded from 2011 – 2020.

River	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020
Arkansas Kaw ¹	0	10	1	0	19	22	64	1	47	39
Arkansas Keystone ¹	0	40	3	0	18	33	57	1	45	51
Cimarron ¹	6	22	11	0	30	15	48	0	66	15
North Canadian	8	10	26	0	38	25	31	17	64	67
Verdigris ¹	9	29	13	0	31	30	45	8	50	51
Washita	5	22	10	0	26	50	35	29	63	62
Red	1	10	0	0	27	38	36	16	80	32

¹Indicates a river system associated with a reservoir with wild recruitment of Paddlefish

Table 11. Mean consecutive days above the 80th percentile of flow from March to May recorded from 2011 – 2020, calculated by dividing the number of days above the 80th percentile divided by the total flow events where there were consecutive days above the 80th percentile in a given spring.

River	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020
Arkansas Kaw ¹	0	3.33	1	0	4.75	4.4	64	1	15.66	7.8
Arkansas Keystone ¹	0	13.33	1.5	0	9	11	14.25	1	15	12.75
Cimarron ¹	3	7.33	2.2	0	15	7.5	24	0	16.5	15
North Canadian	2.66	5	3.71	0	7.6	8.33	7.75	3.4	12.8	11.16
Verdigris ¹	1.8	4.83	2.16	0	7.75	6	9	4	12.5	12.75
Washita	5	3.66	2.5	0	13	6.25	8.75	5.8	15.75	15.5
Red	1	3.33	0	0	9	9.5	9	5.33	40	14

¹Indicates a river system associated with a reservoir with wild recruitment of Paddlefish

Table 12. Hydrology characteristics of study rivers calculated using mean daily discharge values from each river’s respective USGS gage station during the spring (March – May) from 2011 -2020. Values in parentheses represent the SD of the associated mean.

River	Mean daily discharge among years (m ³ /s)	Mean number of days above 80th percentile among years	Mean number of consecutive days above 80th percentile among years
Arkansas above Kaw ¹	50.25 (34.29)	20.3 (22.73)	10.2 (19.48)
Arkansas above Keystone ¹	157.1 (105.76)	24.8 (22.96)	7.78 (6.39)
Cimarron ¹	25.84 (14.49)	21.3 (21.38)	9.05 (8.18)
North Canadian	25.16 (9.37)	28.6 (22.52)	6.24 (3.99)
Verdigris ¹	110.5 (66.7)	26.6 (18.4)	6.08 (4.39)
Washita	59.97 (30.75)	30.2 (22.46)	7.62 (5.48)
Red	70.36 (45.54)	25 (25.25)	9.11 (11.8)

¹Indicates a river system associated with a reservoir with wild recruitment of Paddlefish

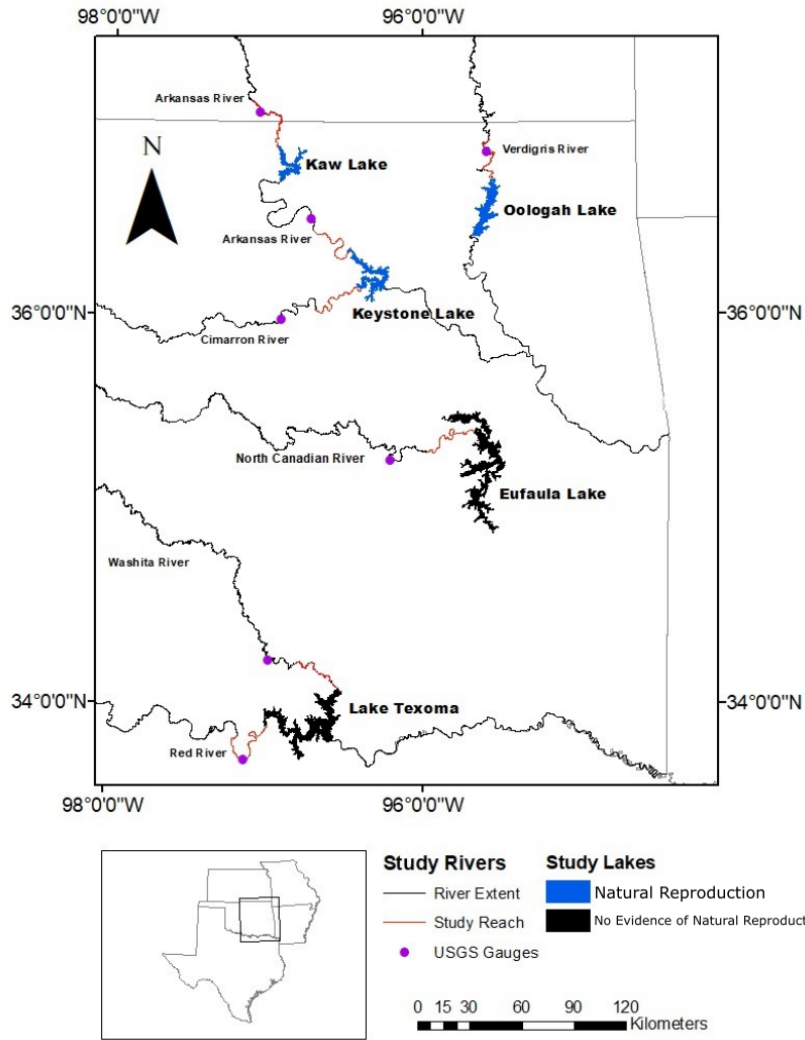


Figure 1. Map illustrating the 50 km study reaches (in red) and their associated river reservoir systems where remote sensing was used to estimate the amount of suitable spawning substrate for Paddlefish.

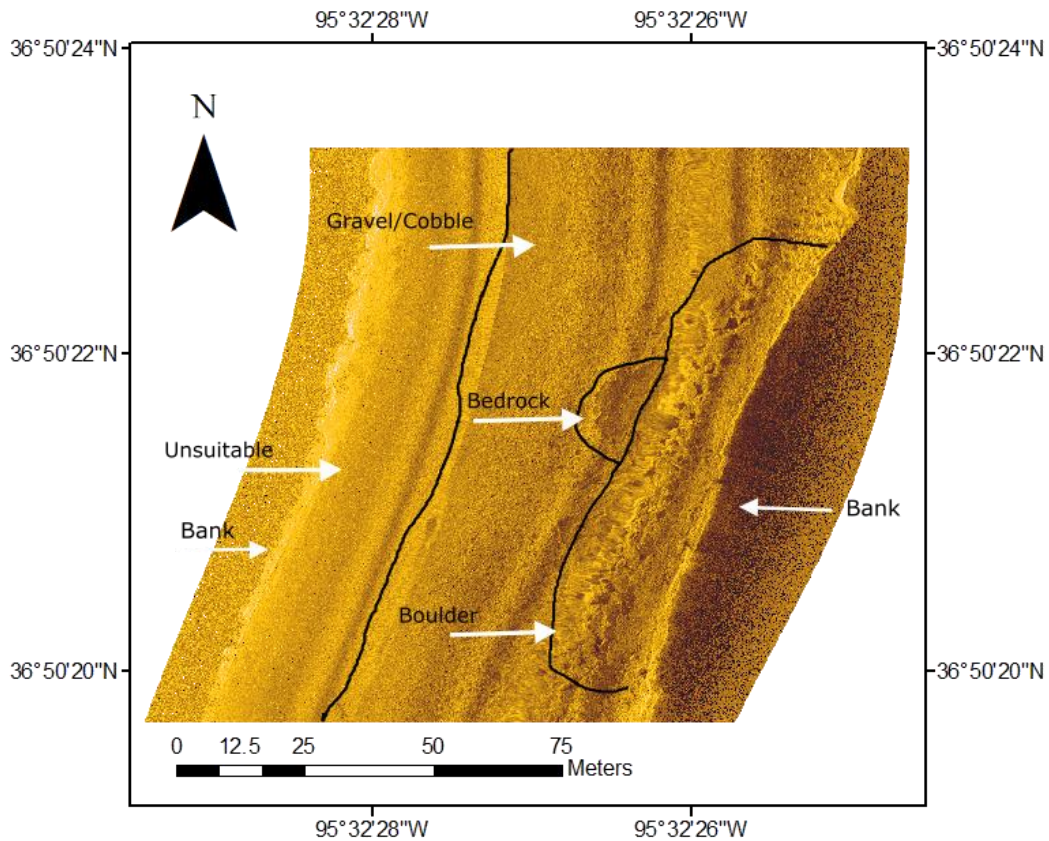


Figure 2. Sonar Imagery as viewed in ReefMaster v2.0 from the Verdigris River and annotated to highlight suitable and unsuitable substrate categories. Black lines have been drawn to outline the boundaries between the substrate categories, river banks can be identified as abrupt margins on either side with little variation in texture, tone or pattern parallel to the margin.

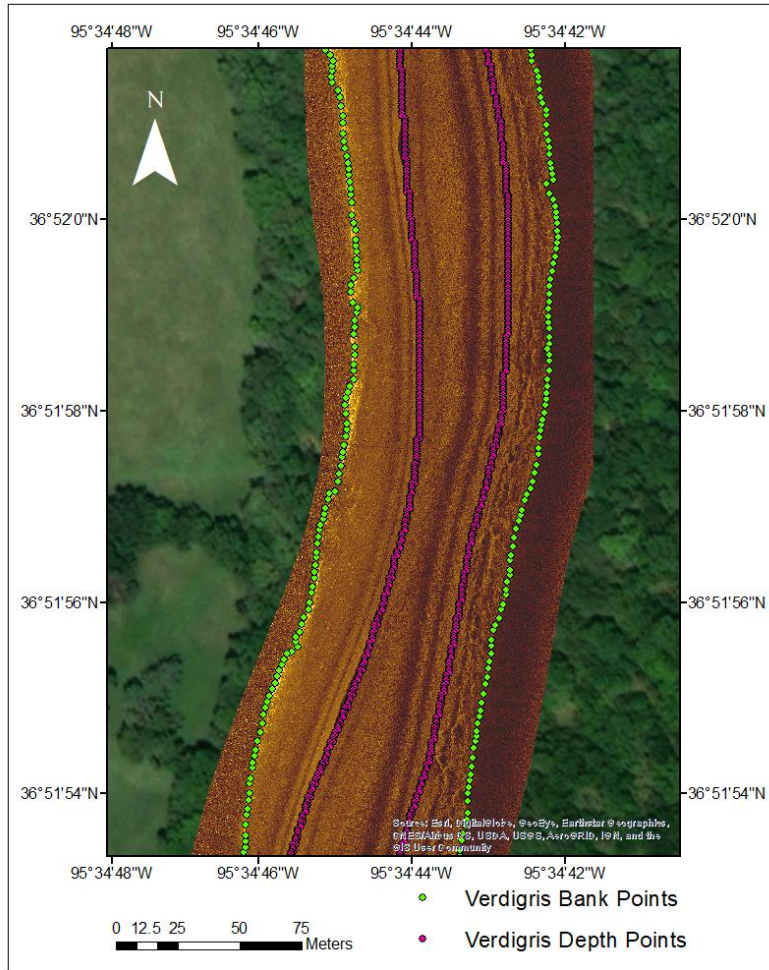


Figure 3. Example from the Verdigris River illustrating points used for TIN creation. Bank points, shown in green, were identified from SSS imagery and placed approximately 2.5 m apart. Depth points, collected from SSS transects shown in purple, were imported from ReefMaster 2.0 and spaced approximately 0.9 m apart.

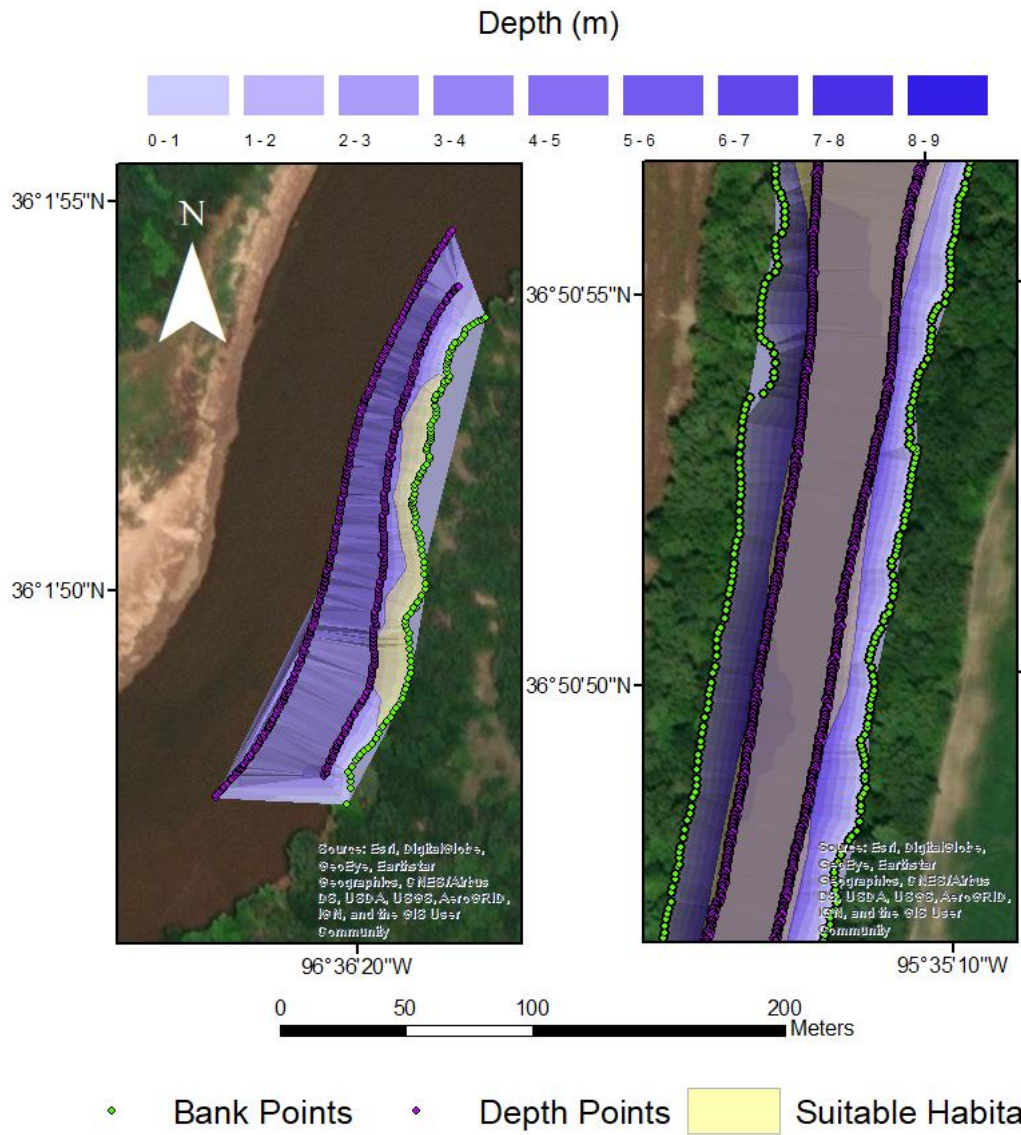


Figure 4. Illustration of our two methods of TIN creation, the Cimarron River (Left) where bank to bank coverage was not possible and Verdigris River (Right) where bank-to-bank coverage was possible.

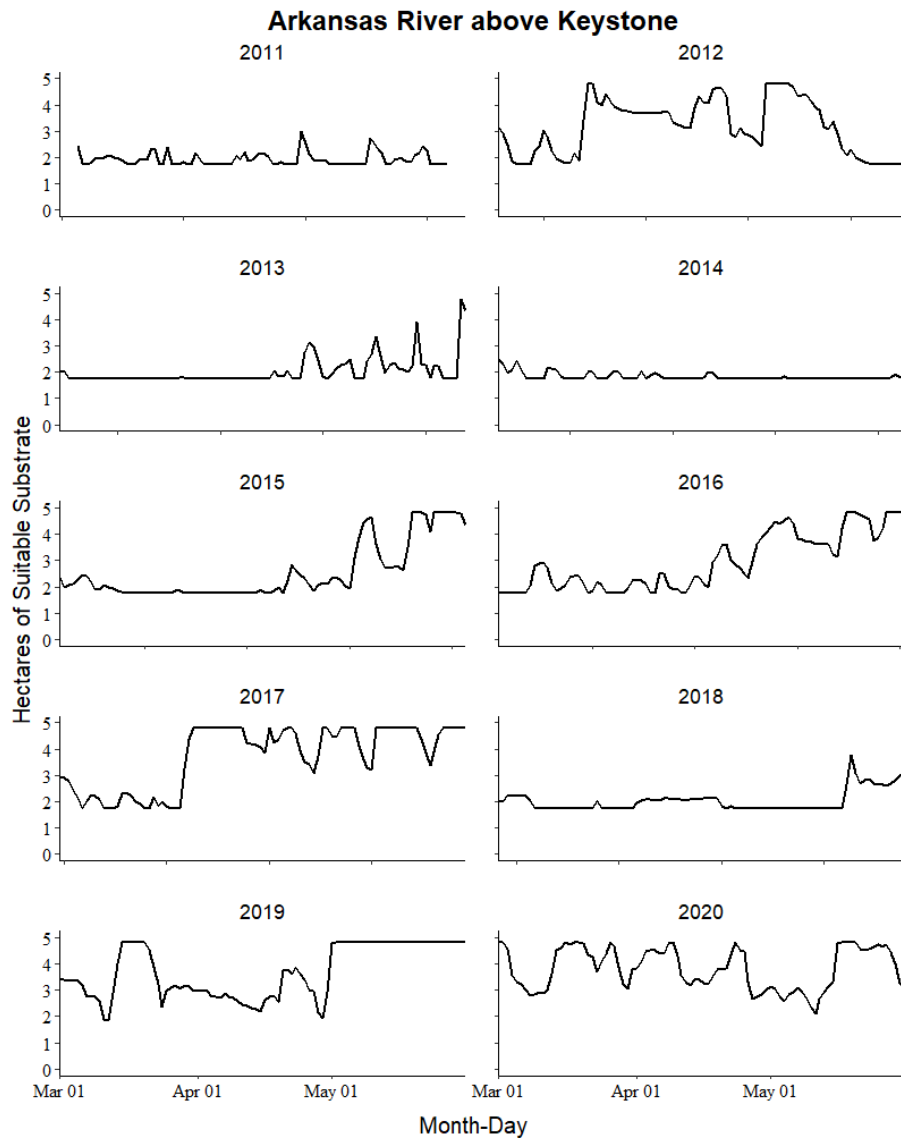


Figure 6. Predicted daily substrate availability from March 1st to May 31st for 2011 to 2020 for the 50 km of the Arkansas River above Keystone Lake as predicted by Substrate-Discharge models.

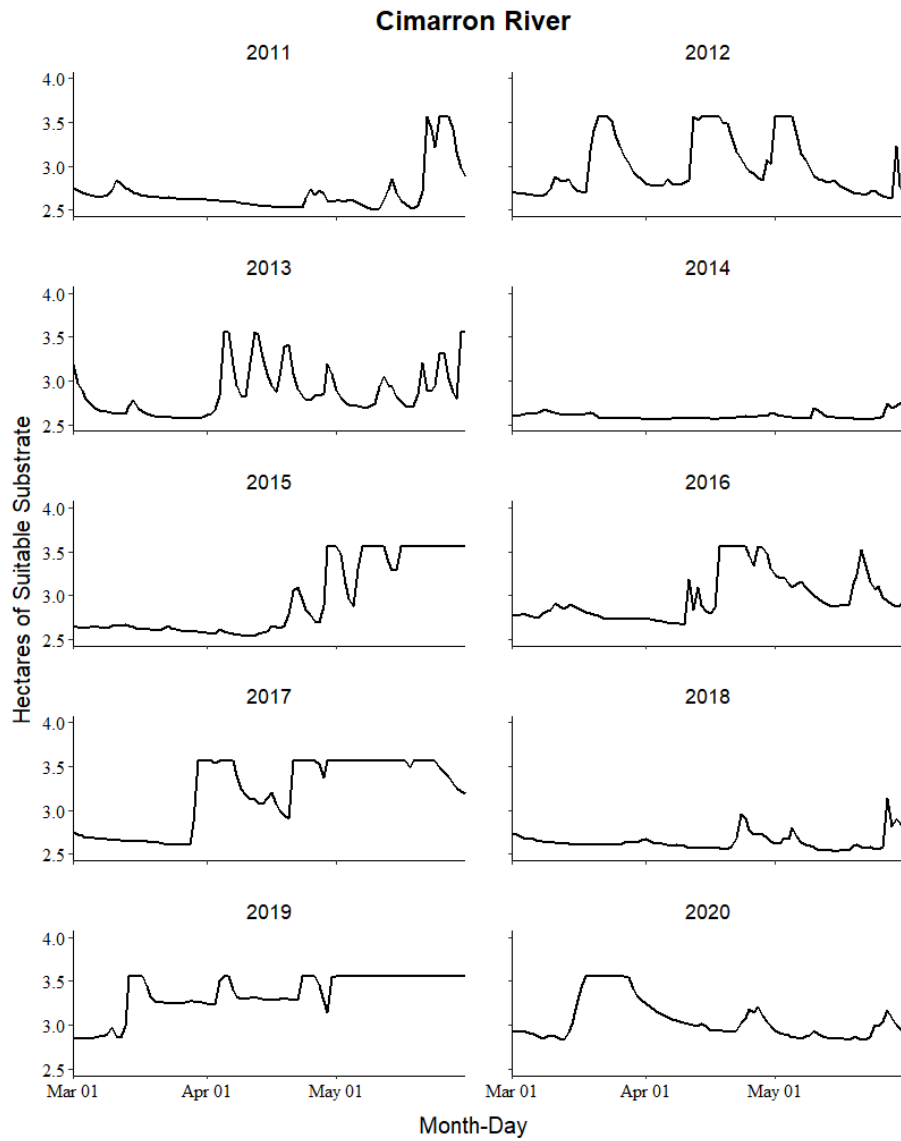


Figure 7. Predicted daily substrate availability from March 1st to May 31st for 2011 to 2020 for the 40 km of the Cimarron River as predicted by Substrate-Discharge models.

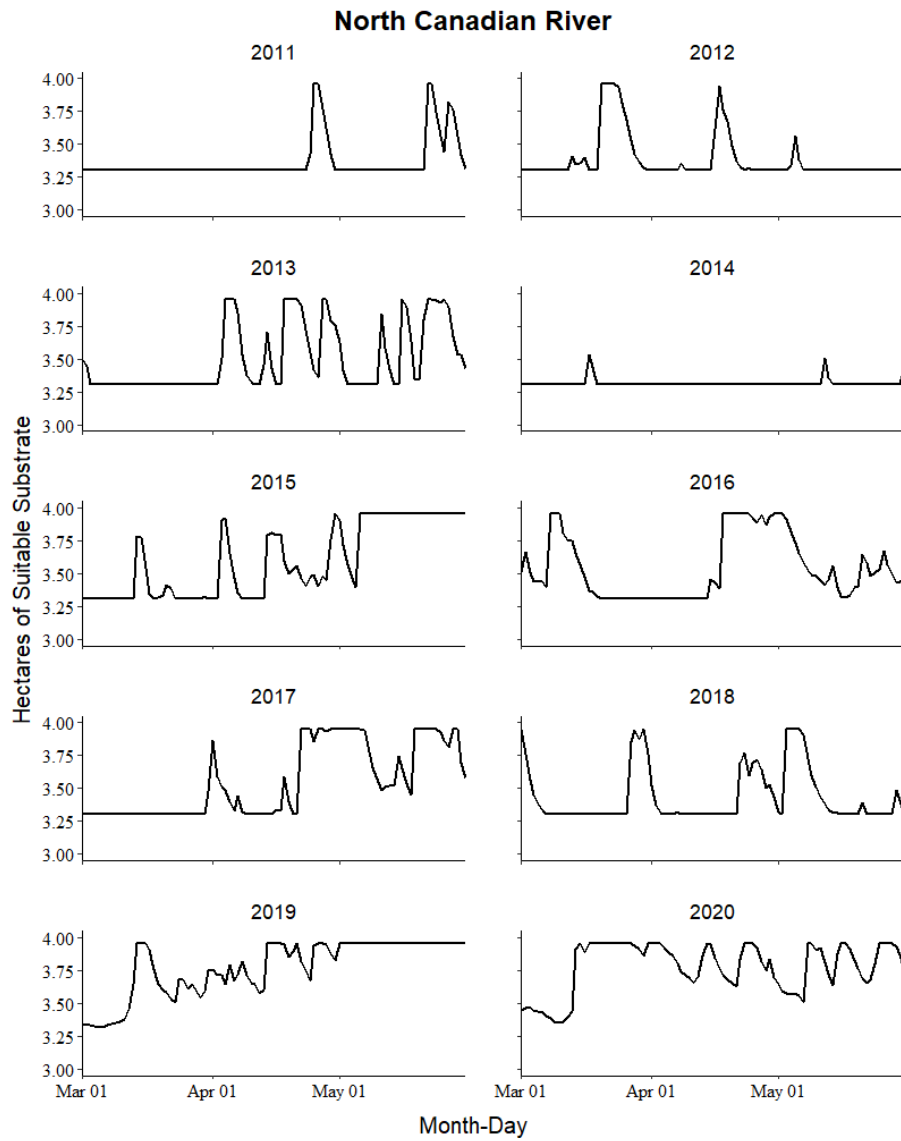


Figure 8. Predicted daily substrate availability from March 1st to May 31st for 2011 to 2020 for the 50 km of the North Canadian River as predicted by Substrate-Discharge models.

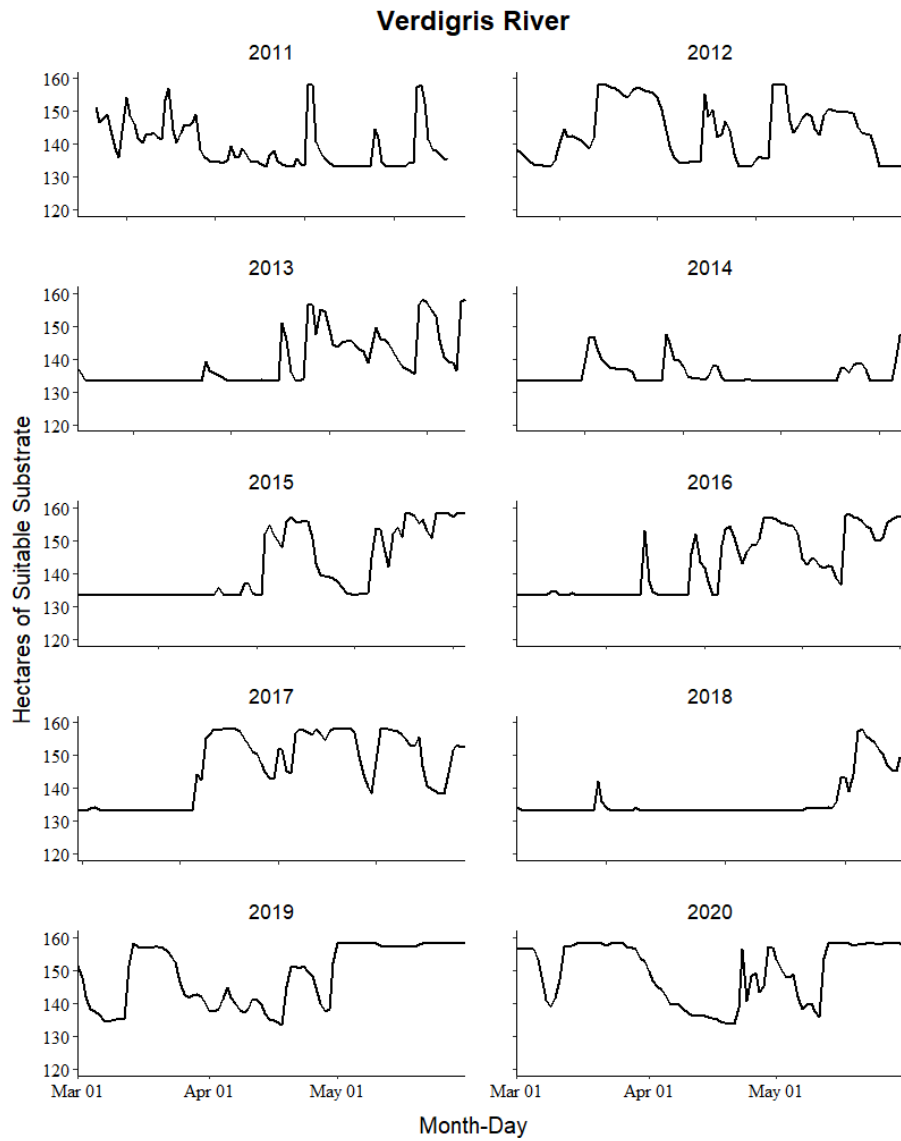


Figure 9. Predicted daily substrate availability from March 1st to May 31st for 2011 to 2020 for the 50 km of the Verdigris River as predicted by our Substrate-Discharge models.

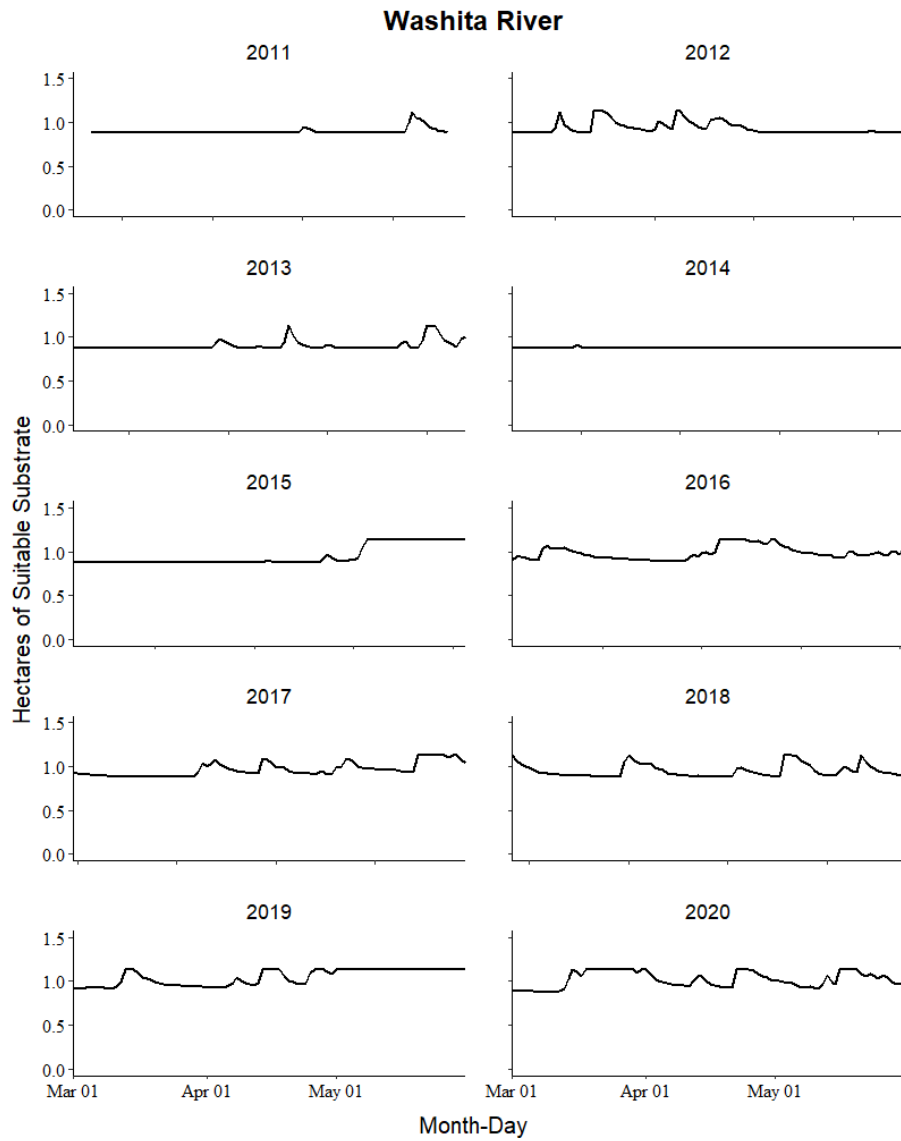


Figure 10. Predicted daily substrate availability from March 1st to May 31st for 2011 to 2020 for the 40 km of the Washita River as predicted by Substrate-Discharge models.

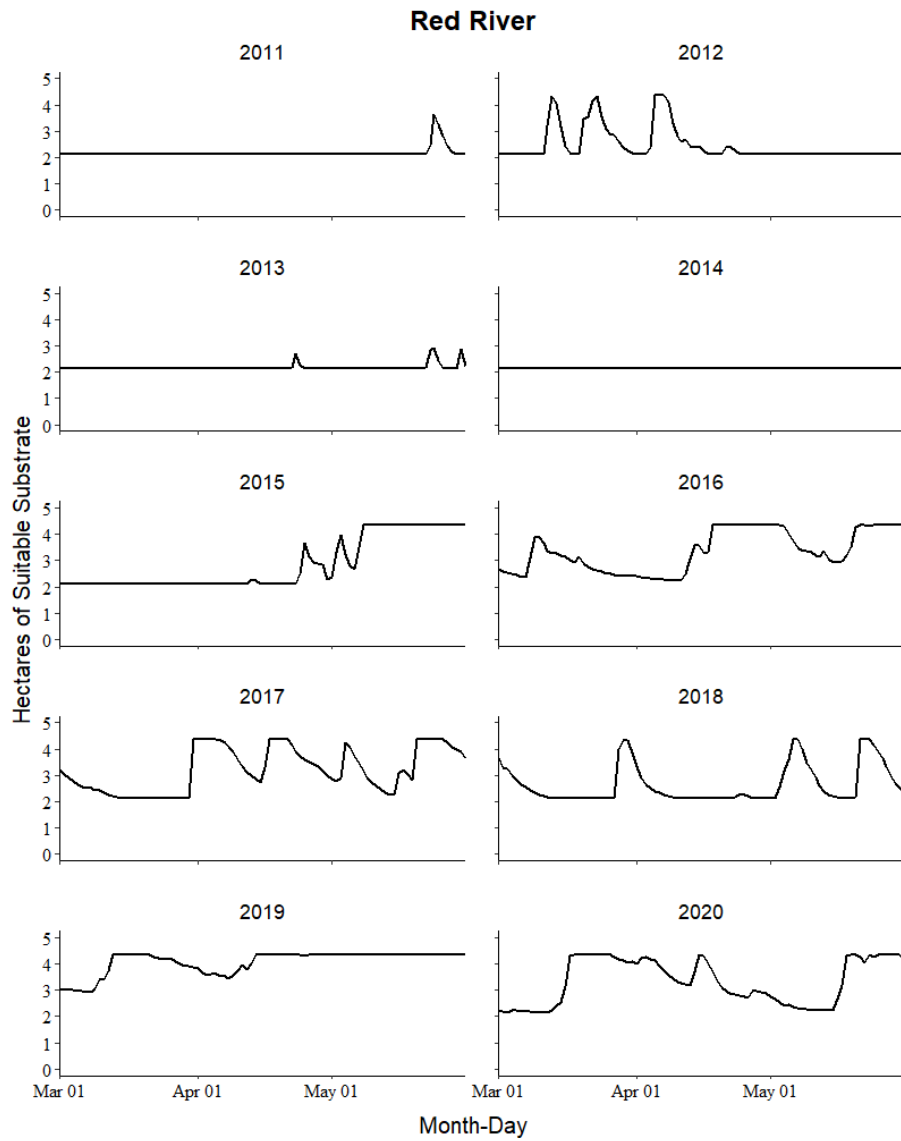


Figure 11. Predicted daily substrate availability from March 1st to May 31st for 2011 to 2020 for the 50 km of the Red River as predicted by Substrate-Discharge models.

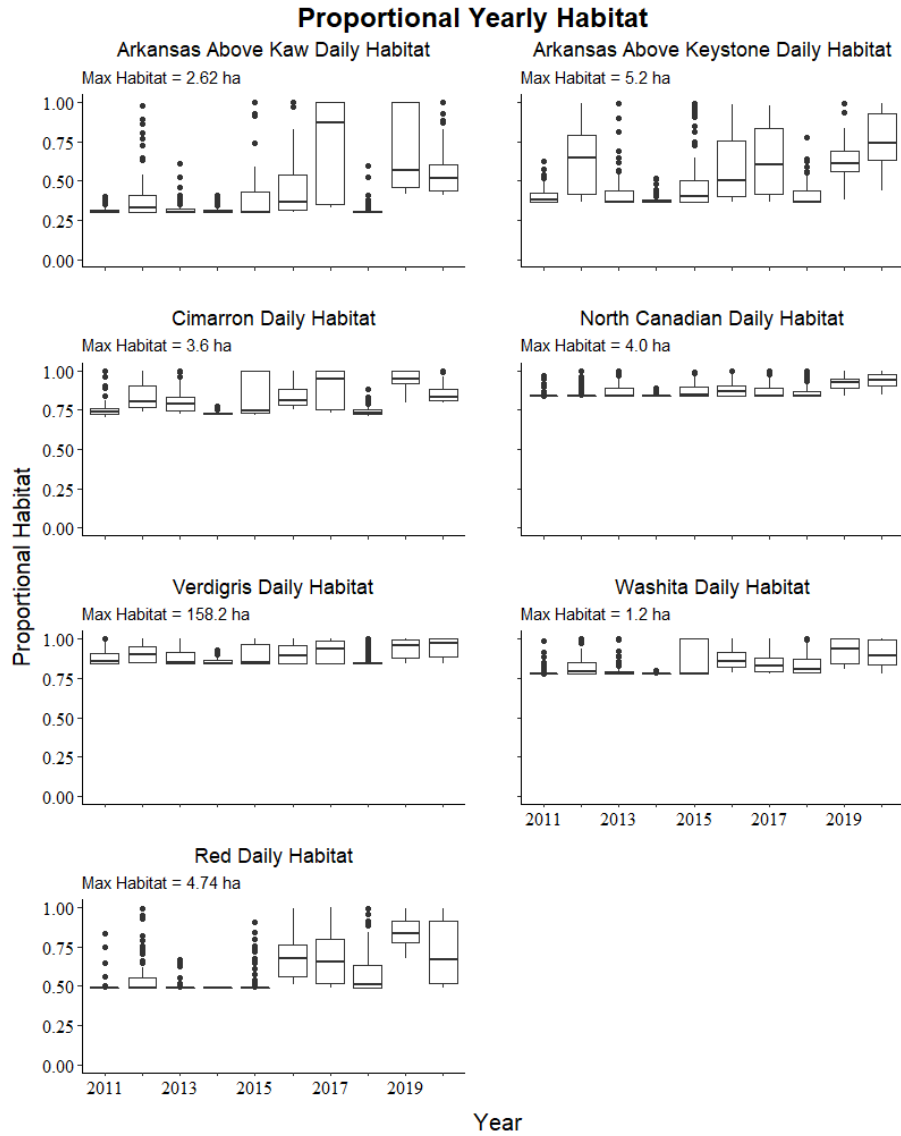


Figure 12. Box plots of proportional habitat from March to May for the years 2011-2020 calculated by dividing daily habitat availability by the habitat available during the maximum discharge value for each river.

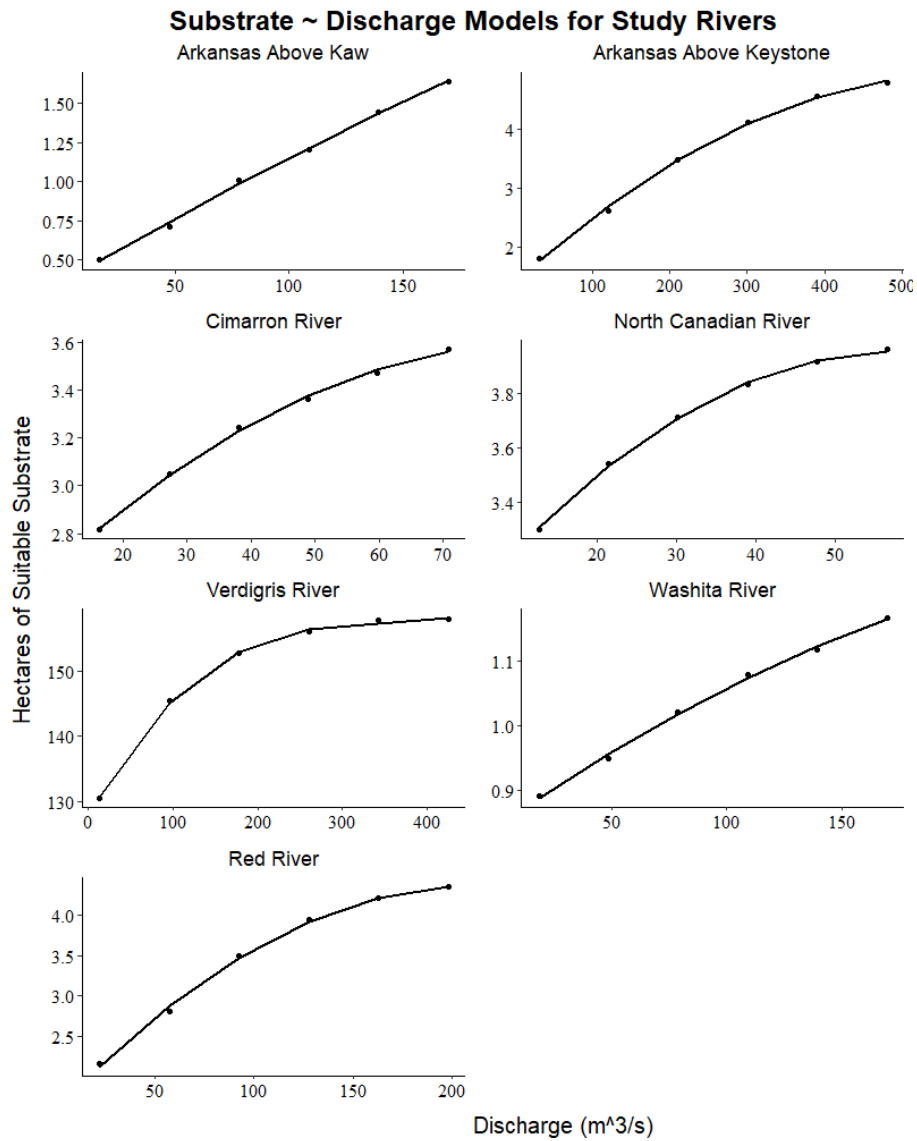


Figure 13. Points of substrate availability at discharge and the subsequent models built from them for each study river (Table 6).

CHAPTER III

CONFIRMATION OF SPAWNING HABITATS USED BY PADDLEFISH IN RESERVOIR TRIBUTARIES

ABSTRACT

Paddlefish are thought to utilize a variety of hard substrates to successfully reproduce in lotic systems. We selected two anthropogenically altered systems that are known to successfully recruit adult Paddlefish, identified by monitoring efforts, but have no current direct evidence of successful spawning. Two sites were selected on the upper and lower portions of contributing reservoir tributaries to Oologah and Keystone Lakes, Oklahoma where we placed up to six passive egg collectors at each site. These sites were chosen by hard substrates identified by side-scan sonar, and local fishing reports where snagging of Paddlefish has been reported. Egg mats were placed during low flows at the beginning of the spring spawning season and checked weekly when flows allowed, or after spikes in discharge. A total of 136 eggs were collected between the two rivers, but only those from the Oologah Lake system (N = 132) were genetically confirmed to be paddlefish.

INTRODUCTION

American Paddlefish *Polyodon spathula* are a highly migratory species native to medium to large free flowing rivers in the Mississippi River drainage and select Gulf slope drainages (Jennings and Zigler 2000). Similar to other potamodromous fishes, they have suffered range loss and population declines during the last century due to anthropogenic threats. Modifications of large rivers such as channelization and the creation of dams are widely cited as primary reasons for these declines (Russell 1986; Sparrowe 1986; Unkenholz 1986; Jennings and Zigler 2000). These modifications alter natural flow regimes that Paddlefish need to induce spawning migrations (Sparrowe 1986; Unkenholz 1986) and inundate necessary spawning substrates that Paddlefish require for successful hatching of eggs (Sparrowe 1986; Unkenholz 1986).

Paddlefish spawning has rarely been directly observed, and the first published account was the observation of fish thrashing at night, followed by the discovery of eggs that were stranded after river levels receded the next day (Purkett 1961). Since Purkett's (1961) work, a consensus of suitable spawning substrate for Paddlefish entails the need for their adhesive eggs to have access to hard substrates on which to attach and continue development before hatching. Gravel and cobble substrates are presumed to be the most suitable for spawning given those were the types observed by Purkett (1961), but larger substrates such as boulder and bedrock are also thought to be suitable provided there is enough current to prevent siltation of eggs (Crance 1987, Jennings and Zigler 2001). However, even after understanding these requirements, few researchers have documented exact areas and times that have led to successful spawning by Paddlefish.

Identifying adequate areas of potentially suitable substrate for Paddlefish spawning is a critical first step in assessing a system's reproductive potential, but verification of successful spawning is a necessary post-requisite to validate suitable spawning substrate. Previous research on Paddlefish has verified successful spawning via collection of drifting larvae and eggs using

active gear (Pasch et al. 1980; Wallus 1986). However, this method is less precise in identifying exact locations and associated substrates where spawning occurs. The use of egg mats placed in areas of potentially suitable spawning substrate, however, allows one to identify not only location, but also confirm timing of spawning when checked regularly and in relation to hydrologic cues thought to initiate spawning (Miller et al. 2008; Miller et al. 2011; Firehammer et al. 2006).

In Oklahoma, the native range of Paddlefish has also been limited by habitat degradation and fragmentation, but the Oklahoma Department of Wildlife and Conservation and the U.S. Fish and Wildlife Service have been actively stocking select reservoirs in an effort to restore lost populations. These select reservoir systems were once within the native range of Paddlefish, but whether they have suitable habitat to create self-sustaining populations are not always known. Two systems, at least, in similar ecoregions have a successfully recruiting populations of Paddlefish (Keystone Lake and Oologah Lake; Graham 1997; Paukert and Fisher 2001; J. Schooley personal communication) and offer an opportunity to examine suitable spawning substrate in more detail. Oologah Lake was stocked with Paddlefish from 1995 to 2000 and evidence of a successful restoration effort was found in 2013 and 2014, although few studies have been conducted since on this population. Keystone Lake has retained a self-sustaining population of Paddlefish since impoundment in 1968, and its population has been studied previously, including reproductive dynamics and location of potentially suitable spawning locations (Paukert et al. 2001; Paukert and Fisher 2001). Using egg mats to sample during the 2020 spawning season we document a spawning event for the first time in a restored population of Paddlefish.

METHODS

Study Area

Keystone Lake is a 9,554-ha reservoir located at the confluence of the Arkansas and Cimarron rivers in northcentral Oklahoma (Figure 1). These two contributing reservoir tributaries differ hydrologically as well as morphologically (Paukert and Fisher 2001). The Cimarron River is a large unimpeded prairie river that flows east from where it originates in New Mexico and has a mean annual discharge of 37 cubic meters per second (m^3/s) immediately upstream of the reservoir. The Arkansas River flowing into Keystone Lake is regulated by discharge from upstream Kaw Dam with a mean annual discharge of 164 m^3/s . Both rivers are wide and shallow braided prairie rivers dominated by sand substrate. Keystone Lake is known to have successful Paddlefish reproduction and has recently produced some of the largest Paddlefish in the state, including the past four state records and the current world record (Graham 1997, Paukert and Fisher 2001, ODWC 2020). While Paddlefish use both rivers for a spawning migration, the majority of the population use the Arkansas River (Paukert and Fisher 2001).

Oologah Lake is a 11,920-ha impoundment of the Verdigris River located just east of Oologah, Oklahoma. The Verdigris River is free-flowing for approximately 245 river km from Toronto Lake near Toronto, Kansas to Oologah Lake and has a mean annual discharge of 81 m^3/s above the confluence with the lake. The Verdigris River is a deep, channelized river with well-defined and stable banks, and the riverbed is made up of rock, shale and bedrock substrate (Wallen 1956). Oologah Lake was stocked with Paddlefish on 17 different occasions between July 1995 and October 2000 totaling 30,458 fish (ODWC unpublished data), and data acquired from the Paddlefish Research Center and ODWC e-check harvest data indicate that over 100 fish have been harvested from the Verdigris River and its tributaries since 2014 (J. Schooley, ODWC, unpublished data). Paddlefish surveys conducted by ODWC in 2013 and 2014 found that 99.7%

of fish collected did not have coded wire tags, indicating they were the product of natural reproduction (J. Schooley, ODWC, unpublished data).

Substrate Surveys

Two areas on each river were chosen for mapping substrate in potential spawning locations, an upstream and downstream site with differing morphological characteristics (Figure 1). Locations were chosen based on angler reports and previous observations of Paddlefish activity in the area. In both rivers, we used side-scan sonar (SSS; Hook 2008, Walker and Alford 2016, Buscombe 2017), consisting of a Humminbird Helix 10 with a bow mounted transducer to map habitat in the spring and summer of 2019. To cover the width of the river with sonar, we completed up to three passes (left, center, and right) at flows of the 75th percentile or greater of mean annual flow. Habitat mapping during these high flow events allowed for the quantification of habitat that would be available to Paddlefish during spikes in discharge that induce spawning events.

Side-scan sonar imagery was imported into ReefMaster v2.0 software to delineate potentially suitable and unsuitable substrates. Polygons were drawn around areas identified as cobble, boulder or bedrock and remaining areas not identified as those three classes of substrate were deemed unsuitable. Habitat polygons were then exported into ArcMap 10.5.1 to be compiled into a final habitat map for further spatial analysis.

In the Arkansas River, which is shallower and wider, we included a supervised classification analysis of aerial imagery at low flows to bolster our SSS habitat maps (Enderle et al 2005; Powell 2009). Aerial imagery acquired from the National Agriculture Imagery Program (NAIP) during their 2013 and 2017 surveys was imported into ArcMap 10.5.1 and analyzed using the maximum likelihood classification tool. These two images allowed us to estimate the extent of submerged substrate at high flows. The NAIP imagery of the Arkansas River from August 20th, 2013 occurred during a high flow event when instantaneous discharge was between 500 m³/s and

600 m³/s (93rd and 96th percentile of mean annual flow, respectively). From this image, we calculated the extent of surface water. The NAIP imagery from November 8th, 2017 represented a low flow event when instantaneous flows were between 18 m³/s and 21 m³/s, (the 22nd and 24th percentile of mean annual flow, respectively). Within the surface water polygon from the high flow event image, we then classified the substrates that were viewable in the low-flow image.

We combined the habitat polygons from SSS imagery and aerial imagery in the Arkansas River as well as SSS imagery habitat polygons in the Verdigris River to create the final habitat maps in ArcMap 10.5.1. In the Arkansas River, where overlap between aerial imagery and SSS imagery occurred, classification by SSS took precedent. Total habitat percentages were then calculated using the projected habitat polygons from the finalized habitat maps.

Egg Mat Design and Implementation

Egg mats for sampling Paddlefish eggs were modified from McCabe and Beckman (1990) for White Sturgeon *Acipenseriformes transmontanus* in the Columbia River, WA and involved PVC pipe (0.15 m diameter and 0.75 m length), covered in furnace filter, filled with sand and capped on both ends to maintain their position on the bottom. Between four and six egg mats were placed at each site in the study rivers during April 2020 (Figure 1).

Mats in the Arkansas River were placed across the width of the channel and were retrieved and deployed by a buoyed float line. Due to high variation in river stage, egg mats on the Verdigris River were tied by float line to permanent structures on the bank to avoid losing mats. Therefore, no egg mats were placed in the mid-channel of this river.

Deployment of egg mats occurred in the spring of 2020 from April 7th until May 1st on the Arkansas River, and from April 4th to May 2nd on the Verdigris River. Egg mats were checked weekly when flows were adequate for access and after spikes in discharge, which Paddlefish use as a cue for spawning (Jennings and Zigler 2001; Figure 2). Egg mats were removed once temperatures exceeded 23°C, the upper thermal threshold for Paddlefish spawning (Hoxmeier and

DeVries 1997). All eggs collected on the mats were removed and placed into vials of 80% ethanol. Eggs were then separated into two categories identified by color and size: likely-Acipenseriformes eggs, which are steely gray or pale yellow and approximately 5 mm in diameter (Miller et al. 2008), and not-likely Acipenseriformes (Firehammer et al. 2006). Likely-Acipenseriformes eggs were counted and a sample from each weekly cohort were sent to the National Fish and Wildlife Forensics Laboratory in Ashland, Oregon for species identification through mitochondrial DNA (mtDNA) analysis.

RESULTS

Classification analysis found a scarcity of hard substrates in the Arkansas River, but an abundance of a variety of potentially suitable habitats in the Verdigris River (Table 1). The Arkansas River upstream site had an average depth of 3 meters and was comprised of 23% boulder substrates. The downstream site had an average depth of 5 meters and was comprised of 2.1% boulder substrates. The remainder was predominately sand, which we considered unsuitable. The upstream site on the Verdigris River had an average depth of 5 meters and was comprised of 30.9% cobble, 38.7% boulder and 5.6% bedrock compared to the downstream site that averaged 8.5 meters in depth and contained 31.8% cobble and 30.1% boulder. The remainder of unsuitable substrates in the Verdigris River was a mixture of clay and silt.

Eggs were found in both river systems, but only the Verdigris River produced eggs that matched the color and size typical of *Acipenseriformes*. In the Arkansas River, a total of 12 egg mats were deployed and they collected 4 eggs (Table 2), none of which corresponded to the size and morphology of *Acipenseriformes* eggs (Figure 3). A total of 10 egg mats were deployed in the Verdigris River, collecting 132 eggs, 124 of which corresponded to the size and color of *Acipenseriformes*. These 124 eggs were collected after high discharge events and most were found from the upper site (Table 2). The upper site on the Verdigris River produced 66 likely-*Acipenseriformes* eggs on the first discharge event, and 47 on the second discharge event. Considering the amount of soak time for egg mats, these 113 eggs correspond to a CPUE of 1.01 eggs per collector-day (Table 3). The downriver site produced 11 likely-*Acipenseriformes* eggs, but only on the second discharge event for a corresponding CPUE of 0.07 eggs/mat/day.

Five samples of four eggs each were sent for genetic analysis: three thought to comprise *Acipenseriformes* eggs (all from the Verdigris River) and two considered not likely to be *Acipenseriformes* (one each from the Arkansas and Verdigris rivers; Figure 3). All analyzed eggs identified as likely *Acipenseriformes* were genetically confirmed to be Paddlefish. Eggs from the

remaining two samples were confirmed to be other than Acipenseriformes, but further testing for identification was not conducted.

DISCUSSION

These results mark the first successful application of egg mats to confirm spawning locations for Paddlefish in Oklahoma. Egg collection on the Verdigris River confirmed what previous data had suggested, that there is a naturally reproducing population indicating restoration efforts in this system were successful. The capture efficiency of eggs, when present, mirrors that of other similar studies. For example, O'Keefe et al. (2007) found 106 eggs in the Tennessee-Tombigbee Waterway using egg mats (CPUE = 0.23 eggs per collector day). In the Yellowstone River upstream of Lake Sakakawea, Miller et al. (2008) found 292 eggs over the course of two years with a cumulative CPUE of 0.15 eggs per collector day. Finally, Miller et al. (2011) found 140 eggs during a two-year study of the Missouri River upstream of Fort Peck Reservoir and had a CPUE of 0.19 eggs per collector day.

Although we did not collect Paddlefish eggs in the Arkansas River, we do not suggest this was indicative of the absence of spawning. Spawning by Paddlefish in the Keystone Lake system, particularly the Arkansas River, is supported by previous studies and monitoring efforts. For example, Paukert (2001) found that Keystone Lake Paddlefish migrated predictably with environmental cues upriver into the Salt Fork of the Arkansas River and the Kaw Dam tailwater. In addition, we can infer successful reproduction in Keystone Lake because there is no stocking, and age structure data consistently indicate multiple year classes, including very young fish (Paukert 2001, Nealis 2006). The lack of positive egg samples in the Arkansas River, thus, seems to be a result of sampling inefficiency as dictated by adverse environmental conditions. The hydroelectric-dominated flow regime coupled with the morphology of a shallow prairie river made it inherently difficult to place and retrieve egg mats. Access to our sites was only safely available by boat during high discharge events, which severely limited the frequency of opportunities for checking egg mats.

Differences in substrates and location of selected sites may have played a role in capture efficiency of eggs. Our upstream site on the Verdigris that collected the most eggs best mirrored the description of preferred spawning habitat (i.e., gravel/cobble bars, Purkett 1961; Crance 1987; Jennings & Zigler 2000). Conversely, the downstream site in the Verdigris River had slightly less hard-bottom habitat. Comparatively, sites selected in the Arkansas River did not fit quintessential definitions of preferred spawning habitat (Purkett 1961) in that much of the substrate was sand with interspersions of boulder for hard substrates that might be suitable for spawning.

By identifying precise locations of Paddlefish eggs, we have better identified where this species spawns, at least in the Verdigris River system. In Oklahoma, others have used a variety of tools to indicate locations where Paddlefish might spawn, but none have been able to provide direct evidence of successful sites of reproduction as we have with egg mats. In this system, we believe this points to the need for further monitoring of Paddlefish reproductive ecology. In Particular, the Verdigris River is well suited for investigations into larval drift requirements, something that is currently unknown and could inform future restoration efforts in impounded rivers similar to those of this study.

In the Arkansas River system, additional work would be required for egg mats to be considered successful. For example, using large-scale mapping techniques and equipment more suited for a shallow prairie system, the Arkansas River can provide insight into how Paddlefish's reproductive requirements are met in an anthropogenically altered system. Furthermore, because Paddlefish are known to concentrate and spawn in tailwaters (Jennings and Zigler 2000), a more thorough study of the Kaw Dam tailwater could identify how this habitat contributes to the maintenance of this population.

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TABLES AND FIGURES

Table 1. Summary of environmental variables at each egg sampling site in the Arkansas and Verdigris rivers, Oklahoma during spring 2020.

	Distance from reservoir interface (km)	Mean depth	
		(m)	% hard substrate
<u>Arkansas River</u>			
Upstream	170	3.0	23
Downstream	10	5.0	2.1
<u>Verdigris River</u>			
Upstream	30	5.0	75.3
Downstream	3	8.5	62.8

Table 2. Number of eggs collected on egg mats by day in spring 2020 in the Arkansas River and Verdigris River, Oklahoma.

Week beginning	Arkansas River		Verdigris River	
	Upstream	Downstream	Upstream	Downstream
10-Apr	0	0		
14-Apr	0	0		
25-Apr			66	0
2-May	0	0	47	11
Total	0	0	113	11

Table 3. Catch per unit effort (CPUE) of Acipenseriformes eggs in the Arkansas and Verdigris rivers, Oklahoma during spring sampling in 2020. Collector-days is equal to the number of egg mats at each site multiplied by the by the amount of days they were deployed.

River	Site	Eggs (N)	Effort (collector-days)	CPUE
Arkansas	Upstream	0	144	0
	Downstream	0	140	0
Verdigris	Upstream	113	112	1.01
	Downstream	11	168	0.068

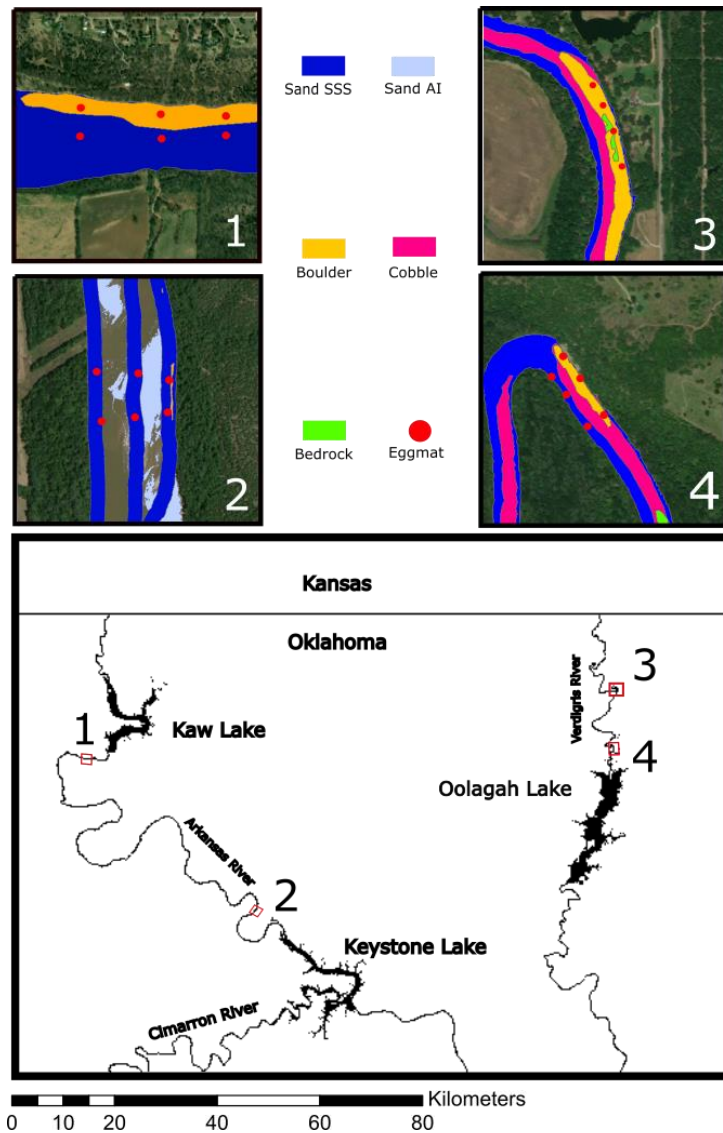


Figure 1. Maps of the Arkansas River between Kaw dam and Keystone Lake in eastern Oklahoma and the Verdigris River in Northeast Oklahoma where egg mats (red circles) were placed for assessing Paddlefish spawning in spring 2019. Light blue represents substrate identified as sand from aerial imagery, whereas dark blue represents sand identified from SSS imagery

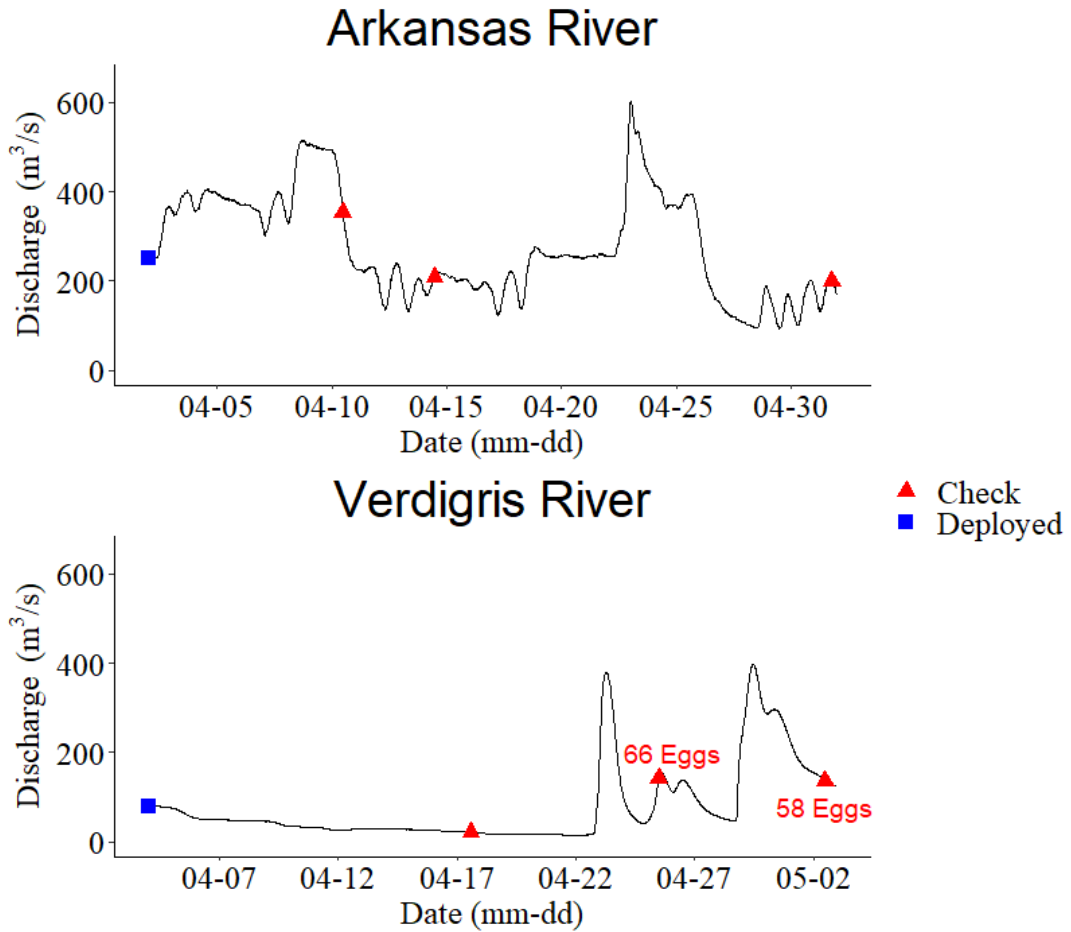


Figure 2. Discharge-time series for the Arkansas (USGS gauge station 07152500) and Verdigris (USGS gauge station 07171000) rivers indicating when egg mats were deployed and checked during the spawning season. Numbers of Paddlefish eggs are indicated above check symbols.



Figure 3. Examples of eggs collected from egg mats, larger eggs were identified as likely Acipenseriformes alongside smaller eggs identified as not likely Acipenseriformes.

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