University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

Characterization of Pallid Sturgeon (*Scaphirhynchus albus*) Spawning Habitat in the Lower Missouri River

Caroline M. Elliott

Aaron J. DeLonay

Kimberly Chojnacki

Robert B. Jacobson

Journal of Applied Ichthyology · DWK · WILEY

Characterization of Pallid Sturgeon (*Scaphirhynchus albus*) Spawning Habitat in the Lower Missouri River

Caroline M. Elliott 🆔 | Aaron J. DeLonay 🆔 | Kimberly A. Chojnacki 🆔 |
Robert B. Jacobson 🆔

Columbia Environmental Research Center, U.S. Geological Survey, Columbia, MO, USA

Correspondence
Caroline M. Elliott, Columbia Environmental Research Center, U.S. Geological Survey, 4200 New Haven Rd, Columbia, MO 65201, USA.
Email: celliott@usgs.gov

Abstract

Acipenseriformes (sturgeons and paddlefish) globally have declined throughout their range due to river fragmentation, habitat loss, overfishing, and degradation of water quality. In North America, pallid sturgeon (*Scaphirhynchus albus*) populations have experienced poor to no recruitment, or substantial levels of hybridization with the closely related shovelnose sturgeon (*S. platorynchus*). The Lower Missouri River is the only portion of the species' range where successful reproduction and recruitment of genetically pure pallid sturgeon have been documented. This paper documents spawning habitat and behavior on the Lower Missouri River, which comprises over 1,300 km of unfragmented river habitat. The objective of this study was to determine spawning locations and describe habitat characteristics and environmental conditions (depth, water velocity, substrate, discharge, temperature, and turbidity) on the Lower Missouri River. We measured habitat characteristics for spawning events of ten telemetry-tagged female pallid sturgeon from 2008–2013 that occurred in discrete reaches distributed over hundreds of kilometers. These results show pallid sturgeon select deep and fast areas in or near the navigation channel along outside revetted banks for spawning. These habitats are deeper and faster than nearby river habitats within the surrounding river reach. Spawning patches have a mean depth of 6.6 m and a mean depth-averaged water-column velocity of 1.4 m per second. Substrates in spawning patches consist of coarse bank revetment, gravel, sand, and bedrock. Results indicate habitat used by pallid sturgeon for spawning is more common and widespread in the present-day channelized Lower Missouri River relative to the sparse and disperse coarse substrates available prior to channelization. Understanding the spawning habitats currently utilized on the Lower Missouri River and if they are functioning properly is important for improving habitat remediation measures aimed at increasing reproductive success. Recovery efforts for pallid sturgeon on the Missouri River, if successful, can provide guidance to sturgeon recovery on other river systems; particularly large, regulated, and channelized rivers.

KEYWORDS

habitat, Missouri River, spawning, sturgeon, telemetry

1 | INTRODUCTION

Nearly all species of Acipenseriformes (sturgeons and paddlefish) are considered highly threatened globally; 24 of the 27 species are listed by the International Union for the Conservation of Nature (Cooke, Paukert, & Hogan, 2012) (https://www.iucnredlist.org/). Sturgeon and paddlefish use large freshwater river systems for spawning, often migrating hundreds of kilometers (km) (Auer, 1996; Bemis & Kynard, 1997). Reasons for the decline of sturgeon worldwide include fragmentation of habitat by dams, commercial fishing, and the degradation of habitat and water quality (Haxton & Cano, 2016; Rochard, Castelnaud, & Lepage, 1990).

The pallid sturgeon (*Scaphirhynchus albus*) is a long-lived, large-river obligate species, native to the swift, turbid waters of the Missouri River, the Middle to Lower Mississippi River and some large tributaries from Montana to the Gulf of Mexico (Jordan et al., 2016; Kallemeyn, 1983). Pallid sturgeon populations declined through the 1900s and the species was listed as endangered under the U.S. Endangered Species Act in 1990 (USFWS, 1990). Habitat loss, altered flow regimes, degraded water quality, and hybridization with the closely related shovelnose sturgeon (*S. platorynchus*) were

identified as the major threats to species survival and recovery. Until recently, researchers have been unable to detect reproduction and recruitment (Dryer & Sandvol, 1993; USFWS, 2014). Given small population sizes with few reproductive adults, the apparent paucity of natural reproduction and recruitment in the Lower Missouri River (LMOR) nearly 30 years after listing is concerning from a species conservation perspective (Steffensen et al., 2019), (Figure 1).

In addition to longitudinal fragmentation by dams, simplification of habitats, and loss of lateral connectivity to the floodplain, it has been hypothesized that specific habitats, such as food producing and rearing habitats for early life stages, and spawning habitat for adults, may have become limited or less than suitable for sufficient population growth (Jacobson, Parsley, et al., 2016). A recent integration and analysis of information related to pallid sturgeon reproductive ecology indicated that rehabilitation of spawning habitat should be among priority management actions to avoid jeopardy to the species in the Missouri River (Jacobson, Annis, et al., 2016).

Previously, the location of pallid sturgeon spawning habitats in the LMOR were unknown and their characteristics undescribed (DeLonay, Chojnacki, Jacobson, Albers, et al., 2016; DeLonay, Chojnacki, Jacobson, Braaten, et al., 2016). Spawning had been
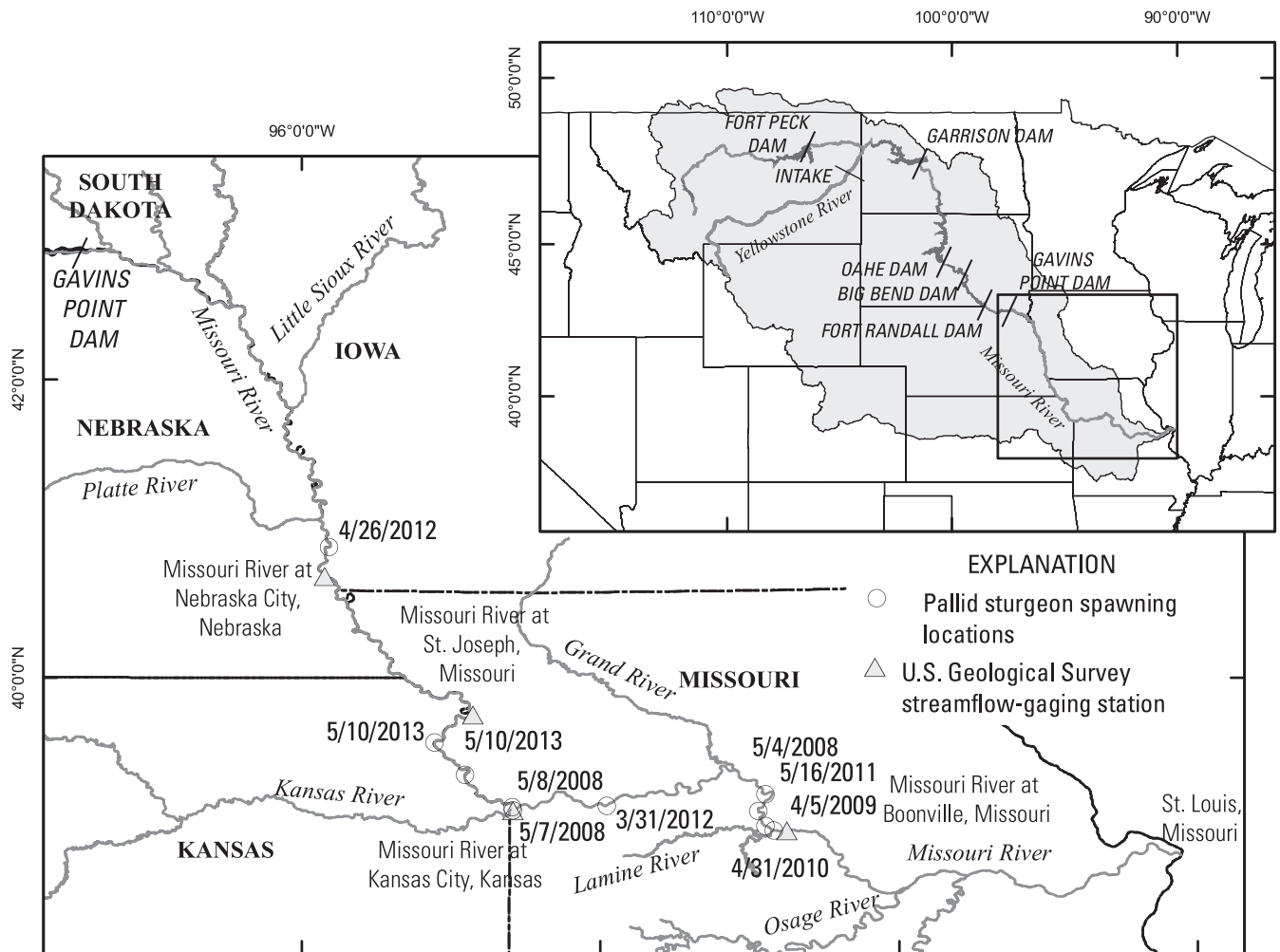

FIGURE 1 Map of the Missouri River basin, Lower Missouri River, and ten pallid sturgeon spawning locations

assumed to occur over coarse substrates in or adjacent to the main river channel (Becker, 1983; Mayden & Kuhajda, 1997), but assumptions were based on analogies to known spawning habitats of other sturgeon species rather than documentation of pallid sturgeon spawning (Dryer & Sandvol, 1993). Most sturgeon species exhibit upstream migratory behavior (Auer, 1996) and spawn in rivers on hard substrates. Sturgeon have been documented spawning over gravel, cobbles, boulders, bedrock, sand, and artificial substrates such as wood pilings, often immediately downstream from a dam (Bruch & Binkowski, 2002; Du et al., 2011; Krykhtin & Svirskii, 1997; Paragamian, 2012; Parsley, Beckman, & McCabe, 1993; Sulak & Clugston, 1998). Spawning habitat hydraulics vary with species and river system; however, many sturgeon species commonly aggregate and spawn in habitat patches with a wide range of depths and relatively high flow velocity (Baril, Buszkiewicz, Biron, Phelps, & Grant, 2017; McAdam et al., 2018; Smith, Smokorowski, & Power, 2017; Wyman et al., 2017). Sturgeon eggs become adhesive several minutes after fertilization and the common inference is that functional spawning substrate for pallid sturgeon is also likely coarse, hard, rock material which allows for stability in high-velocity environments where currents prevent sedimentation (Detlaff, Ginsburg, & Schmallhausen, 1993; Laustrup, Jacobson, & Simpkins, 2007). In high-velocity environments, fertilized eggs may be transported some distance downstream before adhering to coarse substrates or being entrained in interstitial spaces. Lack of knowledge of specific habitat conditions necessary for successful spawning and reproduction of pallid sturgeon limits the ability to define conservation or engineering criteria for habitat protection and rehabilitation efforts (Baril et al., 2017; McAdam et al., 2018; Wang, Xia, & Wang, 2012).

In 2005, the Comprehensive Sturgeon Research Project (CSRP) was initiated to improve the fundamental understanding of reproductive ecology of the pallid sturgeon to inform river- and species-management decisions on the Missouri River. Using acoustic telemetry, from 2007 to 2015, CSRP biologists documented 33 pallid sturgeon spawning events on the LMOR and Platte River, a Missouri River tributary (DeLonay, Chojnacki, Jacobson, Braaten, et al., 2016). LMOR spawning locations are distributed over 950 km of the river from within a few km of Gavins Point Dam to 325 km upstream from the confluence with the Mississippi River in Missouri. Spawning has been detected or inferred through combinations of intensive (hourly to daily) and extensive (weekly to monthly) manual telemetry tracking of reproductive sturgeon. Spawning has been validated through recapture and surgical assessments and depth and temperature information from data-storage tags implanted inside telemetered sturgeon (DeLonay, Chojnacki, Jacobson, Albers, et al., 2016). Of the 33 female sturgeon that spawned, ten were tracked intensively to precise locations during spawning events where we made habitat measurements of depth, velocity, and substrate in the spawning patch and surrounding reach. (Jacobson, Annis, et al., 2016; Wildhaber et al., 2007). In this paper we describe the first observed spawning events for pallid sturgeon in an open river system, and present measurements of sturgeon spawning habitat conditions in a river hundreds of km downstream from main-stem dams.

2 | STUDY AREA

The LMOR flows downstream 1,300 km from Gavins Point Dam on the Nebraska-South Dakota border to its junction with the Mississippi River near St. Louis, Missouri (Figure 1). Gavins Point Dam, constructed from 1952–1957, is downstream from four other large reservoirs in the main-stem Missouri River system and serves to regulate flows for navigation in the 1,200 km downstream from Sioux City, Iowa. Flow alteration on the LMOR has resulted in a reduction in peak flows and an increase of summer low flows (Galat & Lipkin, 2000; Jacobson & Galat, 2008). With increasing distance downstream from Gavins Point Dam, the LMOR achieves a more natural hydrograph with spring rises occurring in most years as large tributaries such as the Platte River (river km 957), the Kansas River (river km 591), and other tributaries enter the LMOR (Galat & Lipkin, 2000; Jacobson & Galat, 2008). The pre-dam, pre-channelization LMOR system was multithreaded and consisted of shifting sandbars, vegetated islands, eroding banks, and backwaters (Jacobson & Galat, 2006). Channelization of the LMOR to maintain a navigation channel and to stabilize banks decreased the river width by 50%–66% and altered river habitats substantially (Funk & Robinson, 1974; Hallberg, Harbaugh, & Witinok, 1979). Channelization included the installation of coarse rock for bank revetment on the banks of outside bends, construction of river-training dike structures in the river on inside bends, and the construction of levees above the banks for flood control. These alterations resulted in a relatively narrow and deep, single-threaded river with few emergent sandbars or islands (Ferrell, 1995). Sand is the prevalent substrate in the LMOR and forms variably sized, migrating dunes, particularly in the navigation channel (Elliott & Jacobson, 2016; Reuter, Jacobson, Elliott, Johnson, & Delonay, 2008).

3 | METHODS

As used in this article, spawning refers to release of eggs by reproductive female fish. Spawning, then, is a *necessary* condition, but is not necessarily *sufficient* for reproductive success and recruitment. Egg release must occur in the presence of reproductive males; eggs need to be fertilized; fertilized embryos need to incubate without being subject to excessive mortality related to predation, sediment deposition, or water quality impairment; free embryos need to hatch into the drift; and larvae need to survive to recruit to the population (Jacobson, Annis, et al., 2016; Wildhaber et al., 2007). Any of the steps in this cascade may be limiting to reproduction and recruitment, but our emphasis is on spawning as egg release and the habitat conditions that influence spawning. We use the term *spawning habitat* to indicate the general hydraulic and substrate conditions associated with spawning. We use the term *spawning patch* to indicate the best achievable delineation of spawning habitat through acoustic telemetry during an actual spawning event; hence spawning patches denote subsets

of spawning habitat. The term *spawning location* refers to the location on the river measured upstream from the junction of the Missouri and Mississippi Rivers to the nearest 10th of a kilometer (or mile) to the centroid of the spawning patch. We use *spawning reach* to indicate the river context around spawning patches; reaches are usually the scale of a bend.

We identified pallid sturgeon spawning locations using acoustic telemetry (MAP RT-A dual port acoustic receiver with directional LHP_1 hydrophones; transmitter model# MM-M-16-50 [77-kHz, 80 × 16 mm, 35 g in air]; Lotek Wireless Inc.) over a 6-year period (2008–2013) (DeLonay, Chojnacki, Jacobson, Albers, et al., 2016; DeLonay, Chojnacki, Jacobson, Braaten, et al., 2016). Reproductive condition of tagged female sturgeon was assessed in the early spring through capture and egg biopsy. A few males were tagged and tracked as part of this study, but due to the large spatial scale of the study and low numbers of fish available for telemetry, female reproductive sturgeon were the main focus of this study. Individual females (and occasionally, males) were manually tracked by boat (hourly to daily) to spawning reaches over weeks to months by field crews from March through June. We recorded coordinates of fish positions using sub-meter differential global positioning systems (DGPS), and a customized ArcPad (ESRI, Redlands, California) mapping application (DeLonay et al., 2009, 2007).

Multiple lines of evidence, including behavior before and during the event in addition to post-event recapture and surgical assessments were used to determine when spawning events occurred. Previous studies indicated pallid sturgeon spawning migrations generally followed an upstream movement pattern over long (>100 km) distances, initiated when water temperatures began to rise above 10°C. Upstream migrating fish generally selected relatively shallow, low-velocity water along inside bends, presumably to minimize energetic expense (McElroy, DeLonay, & Jacobson, 2012). Migration typically culminated with a change in behavior involving short bursts of activity (spawning) in deep, fast water near an outside bend's revetted bank usually at the sturgeon's upstream-most location or migration apex (DeLonay et al., 2014). For the purposes of this study, a spawning event was considered to have occurred once the upstream movement ceased followed by characteristic short bursts of activity in deep, fast water near a revetted bank. Fish telemetry points were recorded with varying intensity during spawning events using manual tracking. We have only included the telemetry points classified as spawning points in this paper and analysis. Spawning telemetry points were recorded over a 1 to 3-day period and include some 24-hr observations when conditions permitted tracking to continue through the night.

The accuracy of manual acoustic telemetry points in the LMOR georeferenced with DGPS varies spatially and temporally with depth, river discharge, and ambient noise associated with sediment transport. With acoustic telemetry, site-specific conditions such as large amounts of bedrock or bank revetment can cause reverberation and multipath of acoustic signals degrading the precision of fish locations near these substrates. Given the sub-meter precision of DGPS and a range of environmental conditions and depths, the accuracy of the telemetry locations in the LMOR is generally 5 m or better in the horizontal direction. The ten spawning events reported in this paper involve female pallid sturgeon intensively tracked during the spawning event, and in all cases, spawning was validated through recapture and reproductive assessments that included the use of ultrasound and/or surgical examination of the ovaries. Dual-frequency identification sonar (DIDSON/ARIS, Sound Metrics, Corp.) was also used opportunistically to validate spawning behaviors.

We used a variety of hydroacoustic tools to map 0.65–2.3 km long reaches centered on spawning patches defined by telemetry positions; the reach-scale maps provide habitat availability. The telemetry fish positions provided habitat use at the patch scale. Spawning reaches were usually mapped within a few days and at a discharge within 10% of that observed during the spawning event. We used a multibeam echosounder, and an acoustic Doppler current profiler (ADCP) georeferenced with a high-resolution real-time kinematic global positioning system (RTK GPS) to map depths and velocities. A sidescan sonar georeferenced with sub-meter DGPS was used to map substrates. Hypack (Xylem, Inc.) survey software was used for navigation and habitat data collection.

High-resolution bathymetry data were collected using a Reson 7125 SeaBat multibeam echosounder (Reson Teledyne Marine), an inertial motion unit, and RTK GPS along longitudinal transects. Multibeam surveys did not include regions within dike fields to prevent equipment damage. Multibeam data were edited using Hypack's Hysweep software, and soundings were exported and gridded to generate maps with a 1-m cell size.

Velocity and depth data were collected using a 1200-kHz Rio Grande ADCP (Teledyne Marine) and RTK GPS (Gaeuman & Jacobson, 2005; Reuter et al., 2008). The ADCP was deployed from a rigid moving-boat mount over cross-sectional transects with a 20-m spacing perpendicular to flow and measured depths as shallow as 0.8 m. ADCP mapping extended across most of the river width, including inside the dike fields, and for this reason the ADCP-derived depth values from each of the 4 ADCP beams were used in the depth-use and availability analysis. Depth-averaged velocities measured by the ADCP were used to evaluate velocities at patch and reach scales. Maps of average water column velocity and ADCP-derived depth data were interpolated and gridded with a 5 m cell size using methods described in detail in Reuter et al., 2008.

Maps of depth-slope were generated from ADCP-derived gridded depth maps using the ArcGIS (ESRI) slope algorithm to calculate the maximum slope of the depth grid within a 3 by 3 cell matrix, in units of degrees. A benthic terrain classification was applied using concepts developed from the Topographic Position Index and Benthic Terrain Modeler (Lundblad et al., 2006; Weiss, 2001). The benthic terrain classification developed for the Missouri River uses depth and slope information to classify the river into crests, depressions, slopes, and flat areas (Reuter, Jacobson, Elliott, & DeLonay, 2009).

Substrate type, classified as sand, revetment, or bedrock, was interpreted from both sidescan sonar imagery and multibeam data. We inferred substrate characteristics in spawning reaches from visually interpreted, mosaicked sidescan sonar data collected in the spawning reach with a 900-khz Marine Sonic Sidescan Sonar towfish (Marine Sonic Technology, Ltd., White Marsh) (Elliott, Jacobson, & DeLonay, 2004; Reuter et al., 2008). We also interpreted substrate from bed textures in gridded and point cloud multibeam data.

Strength of habitat selection was explored using Ivlev's selectivity coefficient (Manly, McDonald, Thomas, McDonald, & Erickson, 2002; Reuter et al., 2009), calculated as:

$$E_i = (o_i - \pi_i) / (o_i + \pi_i)$$

where:

E_i is the selectivity coefficient for resource unit i (from −1 to +1), o_i is the sampled proportion of used habitat units; and π_i is the sampled proportion of available habitat units. Habitat availability was calculated from the full reach maps, selection was derived from the spawning habitat patch values corresponding to spawning telemetry locations. Positive selectivity values indicate selection, values near zero indicate that habitat is used in similar proportion to its availability, and negative coefficient values indicate avoidance.

4 | RESULTS

All 10 pallid sturgeon spawning reaches mapped as part of this work were in the LMOR downstream from Gavins Point Dam between river kms 325 to 934 (Figure 1, Table 1). The upstream-most reach was located just downstream from the confluence with the Platte River on the Nebraska-Iowa border; three reaches were located upstream from the Kansas River; two were located near the Kansas River; and four reaches were clustered near Boonville, Missouri in Central Missouri (Figure 1, Table 1). In most years spawning occurred from late April to mid-May, with the earliest spawn date occurring on March 31, 2012 and the latest on May 19, 2011 (Table 1). There were between 8 and 51 telemetry points classified as spawning points and used for analysis at each spawning location (Tables 2,3). Fish were recaptured as quickly as possible for surgical evaluation, over half of the fish were recaptured between 0–4 days of spawning, and two of the fish evaded recapture until several months after spawning occurred (Table 1).

Spawning occurred over a broad range of discharges, ranging from 1,011–3,823 cubic meters per second, with flow percentiles in the 40th to 91st range for the post-dam flow record, as measured at U.S. Geological Survey streamflow-gaging stations closest to spawning locations (Table 1). Mean daily water temperature during spawning events varied between 15.9 to 19.4 degrees Celsius; and mean water temperature was 17.0 for all spawning events. Turbidity during spawning events was between 50–390 Nephelometric Turbidity Units and is only available for four spawning events that were near gages instrumented to measure turbidity.

Spawning females selected deep water. Mean depth in spawning patches was 4.54–8.54 m, and average mean depth was 6.59 m (Figures 2–4, and Tables 1,2). Ninety percent of the telemetry points recorded during spawning events were in depths >4.15 m and 50% of spawning points were in depths >6.75 m. Mean depths for available habitat (the full mapped area in a reach) across all spawning reaches varied from 3.97 to 6.36 m and mean reach depth was 5.08 m. For all spawning reaches and telemetry spawning points Ivlev's selectivity coefficients were positive, indicating selection at 6.5–11 m, greatest (0.73) at 10.5 m and negative, indicating avoidance for depths <6 m (Figure 3).

Spawning females also selected areas of relatively high depth-averaged velocity near the fastest part of the river in the navigation channel (Figure 2). Mean depth-averaged velocities in spawning patches ranged between 1.28–1.58 m/s, mean velocity was 1.40 m/s. Reach-scale mean depth-averaged velocities were lower, ranging from 1.12–1.39 m/s, mean depth-averaged velocity was 1.25 m/s. The highest mean and maximum depth-averaged velocities in the river were associated with higher discharges, for example in 2010 and 2011, when discharges were in the 88th and 91st flow percentiles (Figures 2 and 4, Tables 1 and 3). The depth-averaged velocity distribution was bimodal in some reaches, where the river has large regions of both high and low velocity (for example near river miles 366.5 and 216.5 [km 589.8 and 348.4] where there is considerable slow water behind wing dikes, Figure 2). Selectivity coefficients indicate spawning patch selection for depth-averaged velocities >1.5 m/s and avoidance of depth-averaged velocities <1 m/s (Figure 4).

Spawning patches consisted of steeper than average bottom slope, with selection for bottom slopes >10° (Figure 5). Slopes >10° make up only 6% of the river but account for 25% of the area of the spawning patches. Selectivity coefficients were high (0.48 to 0.92) for slopes >16.5° (Figure 5). Nearly all spawning occurred in portions of the river classified as depressions (Figure 5). Selectivity coefficients indicate selection for regions classified in the terrain classification as depressions (0.57) and slopes (0.40) and avoidance of flat areas (−0.76) and crests (−0.15) (Figure 5).

Spawning patches were on or adjacent to hard substrates including bank revetment, bedrock, or a combination of both, and to sand (Figure 5). The selectivity coefficient for sand was low (−0.23) and hard substrates was high (0.73) (Figure 5). Artificial bank revetment was present and lined the bank at all spawning locations. Revetment source material varies along the LMOR but consists primarily of angular limestone cobbles and boulders with patches of revetment-derived gravel occurring at the base of the revetment. Revetment slopes are generally around 50%; revetment slope measured from multibeam data at a representative location was between 38%–63%. Outcrops of natural dolomite or limestone bedrock were present in four spawning patches. Two reaches had smaller outcrops of bedrock (near

TABLE 1 Summary of water temperature, discharge, substrate, depth, depth-averaged velocity, and turbidity at pallid sturgeon spawning locations in the Lower Missouri River. (C, Celsius; cms, cubic meters per second; m, meters; m/s, meters per second)

Pallid sturgeon ID number	Spawning dates	Post-spawn recapture evaluation date	River mile[a]	River km[a]	Reach length, in km	Mean water temp., in degrees C	Discharge range, cms	Discharge percentile range	Substrates	Mean depth, m	Mean depth-averaged velocity, in m/s	Turbidity range in NTU's[b]
PLS08-004	5/4/2008-5/5/2008	5/9/2008	230.1	370.3	1.1	15.9	2,390-2,792[c]	79-84	sand, revetment	7.16	1.32	210-390[e]
PLS08-008	5/8/2008-5/9/2008	8/7/2008	366.5	589.8	1.1	17.8	1,611-1,750[d]	61-67	sand, revetment	7.21	1.50	--
PLS08-009	5/7/2008-5/8/2008	7/18/2008	369.5	594.7	0.9	17.0	1,552-1,611[d]	58-61	sand, revetment	6.38	1.37	--
PLS09-007	4/25/2009-4/26/2009	4/26/2009	206.5	332.3	0.9	17.4	1,682[e]	55	sand, revetment	7.56	1.35	50-68[e]
PLS10-006	4/30/2010-5/1/2010	5/11/2010	202	325.6	0.6	16.6	3,823[e]	91	sand, revetment, bedrock	8.54	1.58	--
PLS11-008	5/16/2011-5/19/2011	6/14/2011	216.5	348.4	1.5	17.1	3,341-3,483[c]	88-90	sand, revetment, bedrock	7.42	1.52	--
PLS11-007	3/31/2012	4/3/2012	322.2	518.5	1.3	19.4	1,770[f]	67	sand, revetment	6.53	1.33	--
PLS09-011	4/26/2012	4/27/2012	580	933.7	1.6	16.8	1,076[g]	49	sand, revetment	4.54	1.40	--
PLS08-035	5/10/2013-5/11/2013	5/12/2013	423	680.6	1.9	16.1	1,099-1,161[h]	40-46	sand, revetment, bedrock	5.52	1.30	51-130[h]
PLS13-001	5/10/2013-5/11/2013	5/13/2013	399	642.1	2.3	16.1	1,099-1,161[h]	40-46	sand, revetment, bedrock	5.07	1.28	--
Mean values					1.3	17.0				6.59	1.40	

[a]River miles and kilometers are measured upstream from the confluence with the Mississippi River near St. Louis, Missouri.

[b]Turbidity measurements are in Nephelometric Turbidity Units (NTU's).

[c]Discharge measurements are from the U.S. Geological Survey gaging-station 06906500 Missouri River at Glasgow, Missouri.

[d]Discharge measurements are from the U.S. Geological Survey gaging-station 06893000 Missouri River at Kansas City, Missouri.

[e]Discharge and turbidity measurements are from the U.S. Geological Survey gaging-station 06909000 Missouri River at Boonville, Missouri.

[f]Discharge measurements are from the U.S. Geological Survey gaging-station 06895500 Missouri River at Waverly, Missouri.

[g]Discharge measurements are from the U.S. Geological Survey gaging-station 06807000 Missouri River at Nebraska City, Nebraska.

[h]Discharge and turbidity measurements are from the U.S. Geological Survey gaging-station 06818000 Missouri River at St. Joseph, Missouri.

TABLE 2 Depth in spawning reaches and at telemetry fish locations (spawning patches) recorded during pallid sturgeon spawning events

Entire reach depth map, in meters							Depth at spawning telemetry locations, in meters					
ADCP Depth Map Date	Min.	Max	Range	Mean	SD	Pallid Sturgeon ID number	Number of fish locations	Min.	Max.	Range	Mean	SD
7/10/2008	1.25	10.68	9.43	5.64	1.82	PLS08-004	33	1.84	10.59	8.75	7.16	2.05
5/14/2008	1.12	9.95	8.83	5.34	2.14	PLS08-008	30	2.20	9.53	7.33	7.21	2.16
5/13/2008	1.20	10.22	9.02	5.65	1.41	PLS08-009	43	3.89	8.11	4.22	6.38	0.74
4/26/2009	0.86	13.10	12.24	4.79	2.08	PLS09-007	30	3.71	9.30	5.59	7.56	1.13
5/1/2010	1.91	12.81	10.90	6.36	1.92	PLS10-006	42	3.65	10.32	6.67	8.54	1.18
5/19/2011	0.57	11.56	10.99	5.32	2.63	PLS11-008	49	2.80	9.90	7.10	7.42	1.98
4/14/2012	0.91	10.84	9.93	4.74	1.39	PLS11-007	11	6.17	6.93	0.76	6.53	0.24
5/1/2012	0.72	6.80	6.08	4.14	0.79	PLS09-011	51	3.59	5.32	1.73	4.54	0.41
5/13/2013	0.62	11.89	11.27	4.81	1.60	PLS08-035	21	3.72	8.37	4.65	5.52	0.92
5/15/2013	0.62	9.88	9.26	3.97	1.35	PLS13-001	8	2.86	6.98	4.12	5.07	1.28
Mean values	0.98	10.77	9.80	5.08	1.71		318	3.44	8.53	5.09	6.59	1.21

TABLE 3 Depth-averaged velocity in spawning reaches and at telemetry fish locations (spawning patches) recorded during pallid sturgeon spawning events

Entire reach depth-averaged velocity map, in meters per second							Velocity at spawning telemetry locations, in meters per second					
Velocity Map Date	Min.	Max.	Range	Mean	SD	Pallid Sturgeon ID number	Number of fish locations	Min.	Max.	Range	Mean	SD
7/10/2008	0.18	1.75	1.57	1.13	0.29	PLS08-004	33	0.57	1.62	1.05	1.32	0.27
5/14/2008	0.28	2.28	2.00	1.39	0.36	PLS08-008	30	0.83	1.73	0.90	1.50	0.16
5/13/2008	0.18	2.19	2.01	1.38	0.41	PLS08-009	44	0.87	1.86	0.99	1.37	0.19
4/26/2009	0.32	2.05	1.73	1.23	0.32	PLS09-007	30	0.49	1.58	1.09	1.35	0.26
5/1/2010	0.10	2.04	1.94	1.26	0.41	PLS10-006	42	1.21	1.91	0.70	1.58	0.14
5/19/2011	0.00	2.68	2.68	1.31	0.57	PLS11-008	48	0.33	2.38	2.05	1.52	0.51
4/14/2012	0.06	1.74	1.68	1.13	0.30	PLS11-007	11	1.29	1.38	0.09	1.33	0.03
5/1/2012	0.06	2.03	1.98	1.35	0.42	PLS09-011	51	0.49	1.66	1.17	1.40	0.21
5/13/2013	0.02	1.93	1.91	1.12	0.44	PLS08-035	21	1.03	1.57	0.54	1.30	0.15
5/15/2013	0.00	1.69	1.69	1.17	0.30	PLS13-001	7	0.72	1.55	0.83	1.28	0.24
Mean values	0.12	2.04	1.92	1.25	0.38		317	0.78	1.72	0.94	1.40	0.22

river km 680.6 and 642.1), and two reaches had large outcrops extending up to 50 m into the navigation channel (near river km 348.4 and 325.6). In the spawning patches with extensive bedrock, depths were >7 m and the bottom topography was rough with rocky topographic mounds of bedrock and gravel with up to a 1 m of relief. In the other two patches, bedrock outcrops were less extensive, occurring on banks and in limited areas on the bed. Sand is the dominant substrate in spawning reaches and forms sand dunes near spawning patches that ranged from 0.5 m to 2.6 m high and were 6–60 m long. Repeat measurements of sand dunes made at the spawning patch at river km 332.3 show that sand dunes were actively migrating on the bed of the river over a wide range of discharges (DeLonay, Chojnacki, Jacobson, Braaten, et al., 2016; Elliott & Jacobson, 2016).

5 | DISCUSSION

Pallid sturgeon spawn in deep, high-velocity patches on outside bends adjacent to bank revetment in the contemporary LMOR. Spawning patches are highly modified habitats at the base of, or adjacent to, coarse bank revetment installed during 20th century channelization. The deep, high-velocity habitats near coarse substrates that comprise present-day, pallid sturgeon spawning habitat are common on the LMOR (Bulliner, Elliott, & Jacobson, 2017; Reuter et al., 2008). Deep, high-velocity habitats and coarse substrates were less common in the pre-dam, pre-channelized LMOR, which was characterized by a dynamic, multi-threaded sandy channel, bare sandbars, vegetated islands, eroding banks, and backwaters. Although there are no quantitative habitat
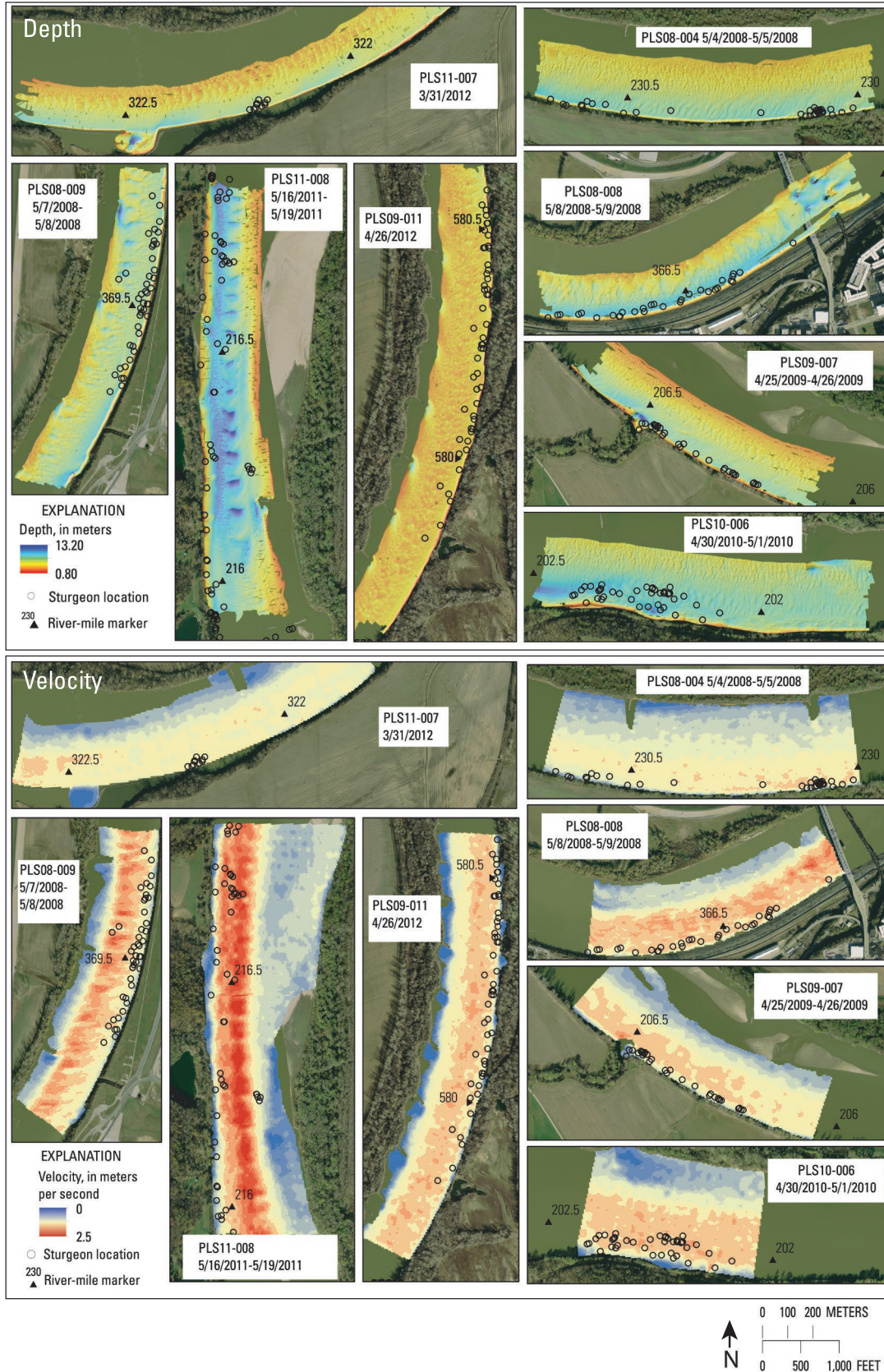
FIGURE 2 Reach-scale maps of depth and velocity of Lower Missouri River spawning locations for the pallid sturgeon identification number indicated on the map. Dates on maps refer to the dates spawning telemetry locations were recorded. Data available at: https://doi.org/10.5066/F7639P23
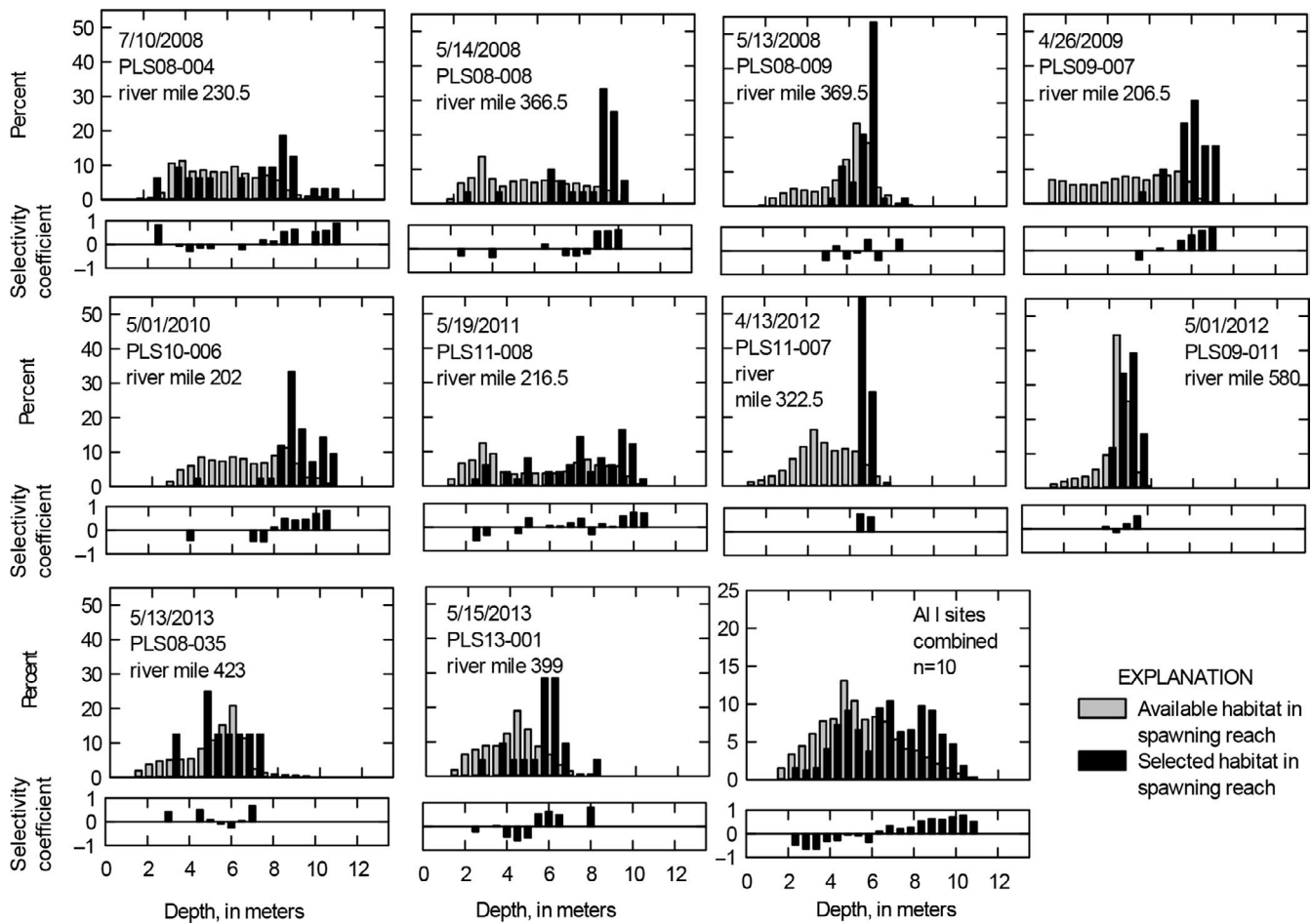
FIGURE 3 Histograms of available and selected depth for pallid sturgeon locations and adjacent reaches in the Lower Missouri River. Pallid sturgeon identification number is indicated for each histogram and dates on histograms are dates of habitat mapping

measurements from the pre-channelized Missouri River, velocities and depths in the relict unchannelized reach between Gavins Point Dam and Sioux City, Iowa are slower and much shallower than spawning habitats selected by pallid sturgeon in the channelized LMOR (Erwin, Jacobson, & Elliott, 2017; Reuter et al., 2009). Pre-channelization, coarse substrates exposed in the river were rare and associated with glacial deposits, coarse-bedded tributary inputs, like the mouths of tributaries draining the Ozark Plateau including the Osage and Gasconade Rivers, or deposits associated with local bedrock outcrops (Laustrup et al., 2007; Reuter et al., 2008). Nearly every outside bend for 1,200 km of the LMOR from St. Louis, Missouri to Sioux City, Iowa is covered in revetment to protect the bank from erosion and to concentrate flow. The channelization of the LMOR may have created an overabundance of spawning habitat. Large amounts of coarse substrates over many kilometers of river may make it difficult for reproductive pallid sturgeon males to form effective aggregations and for females to find suitable mates, possibly contributing to the prevalence of hybridization with shovelnose sturgeon.

Notably, the deep and fast patches on outside bends that pallid sturgeon select for spawning are quite different from the habitats selected during their upstream reproductive migrations on the LMOR

prior to spawning (McElroy et al., 2012). During reproductive migrations, which may be 100's of km, pallid sturgeon generally seek to minimize energy expenditures by moving upstream along the inside bends where the water is slower and shallower. When they reach the upstream extent of an inside bend, they ferry through the cross-over, moving nearly perpendicular to the current, until they encounter the slower water on the opposite side of the river, where they resume upstream movement (McElroy et al., 2012). Transition from selection of slow, shallow water to deep, fast water underscores the importance of understanding habitat selection for specific life-stage functions. Habitat selection for regions of high bottom slope is consistent with habitat use trends for migrating reproductive female shovelnose sturgeon on the LMOR; unlike our study, the shovelnose sturgeon studies did not differentiate spawning habitat from migratory habitat (Bonnot et al., 2011; Reuter et al., 2009).

The channelized LMOR's artificially emplaced bank revetments and gravels may provide poor quality or non-functional habitats for spawning and embryo incubation. Interstitial spaces in bank-revetment or associated gravels may not be adequate for embryo adhesion and incubation. Constant movement of sandy bedforms in and adjacent to spawning patches presents a potential disturbance to embryo deposition and incubation. Repeat
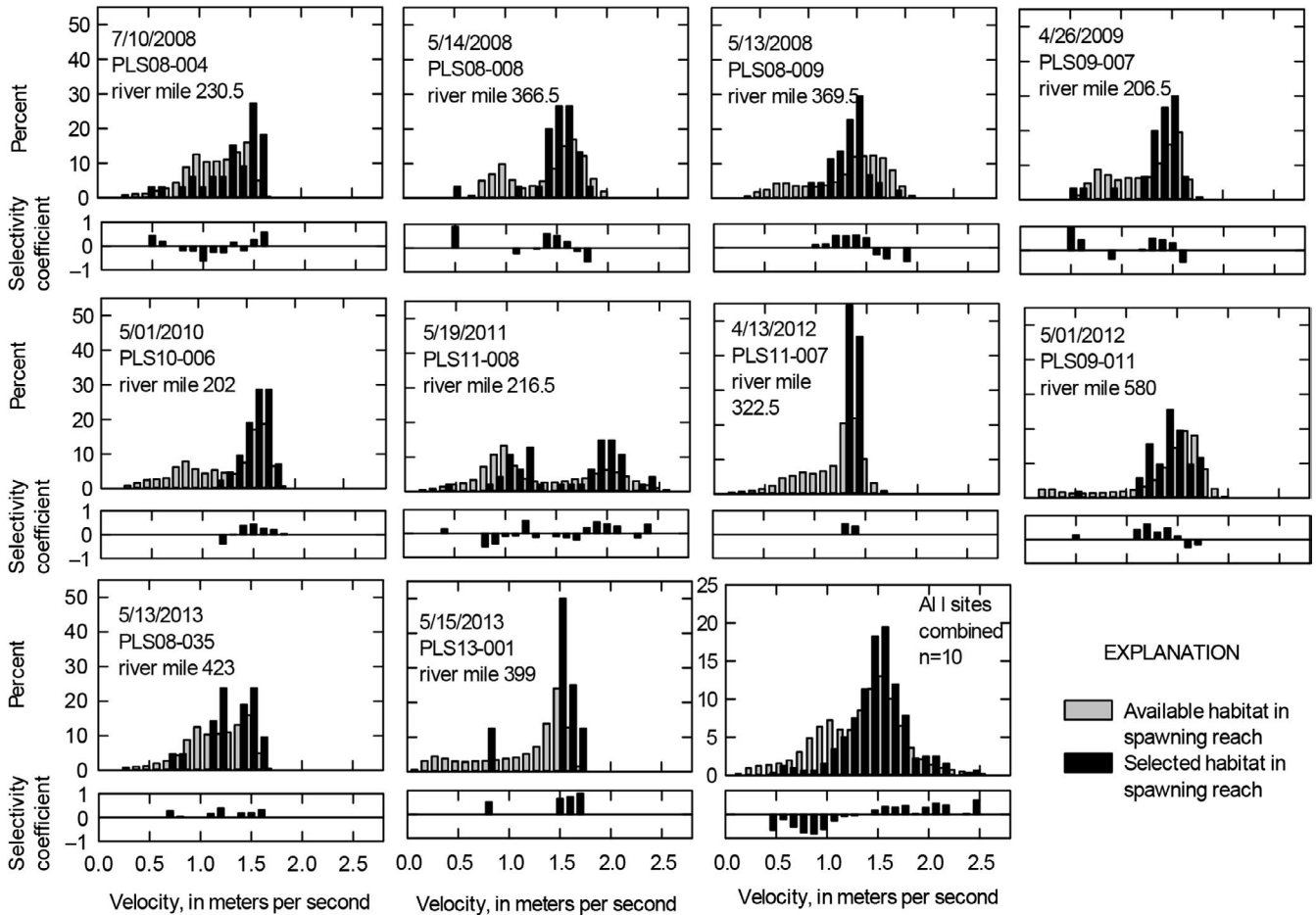
FIGURE 4 Histograms of available and selected depth-averaged velocity for pallid sturgeon locations and adjacent reaches in the Lower Missouri River. Pallid sturgeon identification number is indicated for each histogram and dates on histograms are dates of habitat mapping
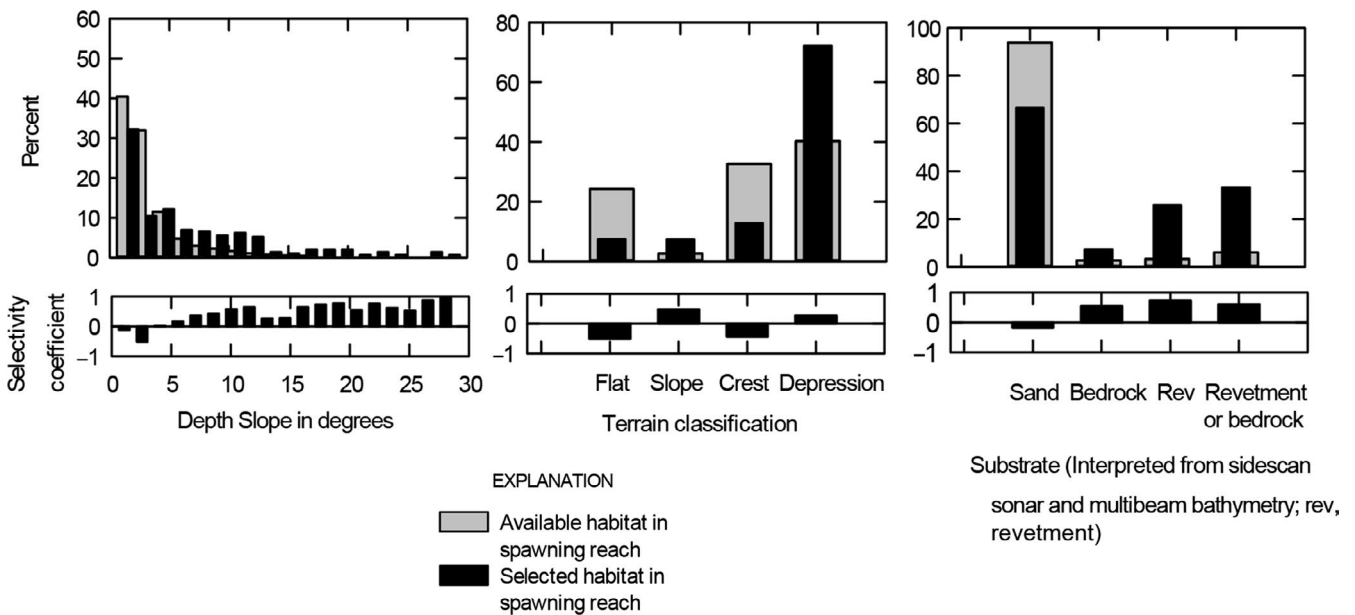

FIGURE 5 Histograms of available and selected depth slope, terrain classes, and substrates for pallid sturgeon locations and adjacent reaches in the Lower Missouri River

measurements on revetment and bedrock substrates at spawning patches demonstrate that areas of these coarse substrates can be stable and free of sedimentation over the time frames of spawning and egg incubation (DeLonay, Chojnacki, Jacobson, Braaten, et al., 2016; Elliott & Jacobson, 2016). However, migrating sand dunes and stable revetment or bedrock are directly adjacent in spawning patches. Exactly where eggs are released and deposited remain critical uncertainties.

Spawning in the contemporary LMOR occurs in a relatively narrow zone between stable coarse substrate on revetted banks and a highly dynamic, mobile sand bed. The fate of embryos under these conditions is unknown, and has been assumed that embryos deposited on sand will become buried by dunes within hours due to high sediment transport rates (Elliott & Jacobson, 2016). Laboratory studies have shown low survival and development rates for white sturgeon embryos buried in sand (Kock, Congleton, & Anders, 2006). Emerging laboratory data for pallid sturgeon, however, indicate with the exception of complete burial by sand some survival can be expected (Chojnacki, George, & DeLonay, 2017).

Field assessments of embryo deposition in LMOR spawning patches remain a challenge because of difficulties associated with identifying precisely where embryos are released and how far they may be transported before adhering to substrate. Furthermore, the time it takes embryos to become adhesive in a turbid, turbulent river environment is unknown. Turbidity conditions during spawning events were variable; moderate compared to the high range of variability in turbidity that can occur on the LMOR, and lower than pre-dam and channelization historical measurements from 1907 (Blevins, 2006). Laboratory, flume, and mesocosm studies of embryo adhesion characteristics and transport could resolve some of these uncertainties.

High-resolution telemetry using two-dimensional acoustic arrays, or the implementation of event-based tags to record egg expulsion events could potentially be used to document spawning and embryo deposition with enough precision to determine if they are deposited on bank revetment, in gravel or sand at the base of bank revetment, on bedrock, on gravel associated with bedrock outcrops, or within migrating sand dunes. Pallid sturgeon also spawn near the river bed where flow separation and complex turbulence associated with sand dunes and revetment create highly variable velocity fields. ADCP's similar to those used in this study are not capable of measuring velocities in the bottom-most 25–50 cm. Improved instrumentation is needed to more precisely measure patch conditions near the substrate to more accurately assess habitat selection and embryo transport and fate.

Despite low numbers and poor recruitment, the LMOR is the only portion of the pallid sturgeon's range where spawning, reproduction, and recruitment of genetically pure pallid sturgeon has been documented (Jordan et al., 2019). Intensive study of known spawning patches, however, has provided little evidence of successful reproduction — measured as hatch of fertilized embryos and downstream dispersal of free embryos. Sampling for drifting free embryos downstream from the ten suspected spawning patches captured only one potential hybrid pallid sturgeon x shovelnose sturgeon free embryo (DeLonay et al., 2014). This was immediately downstream from the May 16–19, 2011 spawning location near river km 348. Lack of documented reproductive success at these patches is consistent with the hypothesis that they may be of poor quality and lack some characteristics necessary for survival from embryo deposition through hatch.

The Pallid Sturgeon Effects Analysis and Missouri River Science and Adaptive Management Plan introduced the hypothesis that spawning habitat quality (among other potential limitations) may be limiting reproduction and recruitment on the LMOR; subsequently the Missouri River Recovery Program has prioritized the design and construction of improved spawning habitat for pallid sturgeon (Fischenich, Buenau, et al., 2018; Jacobson, Annis, et al., 2016). Very little design guidance exists for functional spawning habitat in the LMOR. Spawning habitat construction and remediation efforts, particularly for lake sturgeon, have shown variable rates of success (McAdam et al., 2018). It is unclear the extent these rehabilitation efforts translate to LMOR and to pallid sturgeon, although there is value in lessons to be learned from less successful or failed restoration projects (Baril, Biron, & Grant, 2019). Repeated aggregations and spawning of pallid sturgeon have been documented on the Lower Yellowstone River in a reach that is wider and shallower than the LMOR, and which consists of mostly sand substrate (DeLonay, Chojnacki, Jacobson, Albers, et al., 2016). Low numbers of pallid sturgeon free embryos have been captured directly downstream from known spawning patches on the Lower Yellowstone, indicating that spawning habitat there is somewhat functional. If Yellowstone River spawning patches represent optimal habitat conditions, it is not clear if they would be compatible with the channelized LMOR. Further research into spawning habitats and reproductive behavior of pallid sturgeon in the Lower Yellowstone River, and other portions of the species range where spawning occurs, may provide useful guidance in design of functional spawning habitat on the LMOR. Additional adult telemetry, free-embryo and larval sampling, and hydraulic modelling of downstream dispersal and retention of early life stages have been identified in the Missouri River Science and Adaptive Management Plan as science priorities to improve understanding of spawning and the role of spawning habitats in reproduction and recruitment (Fischenich, Buenau, et al., 2018; Fischenich, Marmorek, et al., 2018).

In summary, this effort presents increased understanding in spawning behavior and the locations of spawning habitats used by pallid sturgeon in an open river system many km downstream from main-stem dams. Downstream from LMOR spawning locations, hundreds of km of free-flowing river on the LMOR and Mississippi Rivers are potentially available for larval development and drift. Although information gaps remain, this is the first study to present detailed quantitative measurements and maps of sturgeon spawning locations and habitat in a large, regulated, and channelized river, hundreds of km below a dam.

DATA AVAILABILITY STATEMENT

The habitat data files identified in this report are part of a USGS data release and can be found on Science Base. https://doi.org/10.5066/F7639P23

ORCID

Caroline M. Elliott https://orcid.org/0000-0002-9190-7462
Aaron J. DeLonay https://orcid.org/0000-0002-3752-2799
Kimberly A. Chojnacki https://orcid.org/0000-0001-6091-3977
Robert B. Jacobson https://orcid.org/0000-0002-8368-2064

REFERENCES

Auer, N. A. (1996). Importance of habitat and migration to sturgeons with an emphasis on lake sturgeon. _Canadian Journal of Fisheries and Aquatic Sciences_, _53_(Suppl. 1), 152–160. https://doi.org/10.1139/f95-276

Baril, A., Biron, P. M., & Grant, J. W. A. (2019). An assessment of an unsuccessful restoration project for lake sturgeon using three-dimensional numerical modelling. _North American Journal of Fisheries Management_, _39_(1), 69–81. https://doi.org/10.1002/nafm.10250

Baril, A., Buszkiewicz, J. T., Biron, P. M., Phelps, Q. E., & Grant, J. W. A. (2017). Lake Sturgeon (_Acipenser fulvescens_) spawning habitat: A quantitative review. _Canadian Journal of Fisheries and Aquatic Sciences_, https://doi.org/10.1139/cjfas-2017-0100

Becker, G. C. (Ed.) (1983). Sturgeon family: Acipenseridae. In _Fishes of Wisconsin_ (pp. 219–237). Madison, WI: University of Wisconsin Press. Retrieved from http://digital.library.wisc.edu/1711.dl/EcoNatRes.FishesWI

Bemis, W. E., & Kynard, B. (1997). Sturgeon rivers: An introduction to acipenseriform biogeography and life history. _Environmental Biology of Fishes_, _48_(1), 167–183. https://doi.org/10.1023/a:1007312524792

Blevins, D. W. (2006). _The response of suspended sediment, turbidity, and velocity to historical alterations of the Missouri River._ U.S. Geological Survey Circular 1301.

Bonnot, T. W., Wildhaber, M. L., Millspaugh, J. J., DeLonay, A. J., Jacobson, R. B., & Bryan, J. L. (2011). Discrete choice modeling of shovelnose sturgeon habitat selection in the Lower Missouri River. _Journal of Applied Ichthyology_, _27_(2), 291–300. https://doi.org/10.1111/j.1439-0426.2010.01637.x

Bruch, R. M., & Binkowski, F. P. (2002). Spawning behavior of lake sturgeon (_Acipenser fulvescens_). _Journal of Applied Ichthyology_, _18_(4–6), 570–579. https://doi.org/10.1046/j.1439-0426.2002.00421.x

Bulliner, E. A., Elliott, C. M., & Jacobson, R. B. (2017). _Acoustic Doppler current profiler raw measurements on the Missouri and Yellowstone rivers, 2000-2016, Columbia Environmental Research Center._ U.S. Geological Survey data release.

Chojnacki, K. A., George, A. E., & DeLonay, A. (2017). _Effects of sediment cover on survival of developing Scaphirhynchus sturgeon embryos._ Nebraska City, NB. Paper presented at the Missouri River Natural Resources Conference.

Cooke, S. J., Paukert, C., & Hogan, Z. (2012). Endangered river fish: Factors hindering conservation and restoration. _Endangered Species Research_, _17_(2), 179–191. https://doi.org/10.3354/esr00426

DeLonay, A. J., Chojnacki, K. A., Jacobson, R. B., Albers, J. L., Braaten, P. J., Bulliner, E. A., & Wildhaber, M. L. (2016). _Ecological requirements for pallid sturgeon reproduction and recruitment in the Missouri River: A synthesis of science, 2005–2012._ U.S. Geological Survey Scientific Investigations Report 2015–5145.

DeLonay, A. J., Chojnacki, K. A., Jacobson, R. B., Braaten, P. J., Buhl, K. J., Elliott, C. M., & Mestl, G. E. (2016). _Ecological requirements for pallid sturgeon reproduction and recruitment in the Missouri River: Annual report 2014._ U.S. Geological Survey Open-File Report 2016–1013.

DeLonay, A. J., Jacobson, R. B., Chojnacki, K. A., Annis, M. L., Braaten, P. J., Elliott, C. M., & Wildhaber, M. L. (2014). _Ecological requirements for pallid sturgeon reproduction and recruitment in the Missouri River: Annual report 2011._ U.S. Geological Survey Open-File Report 2014–1106.

DeLonay, A. J., Jacobson, R. B., Papoulias, D. M., Simpkins, D. G., Wildhaber, M. L., Reuter, J. M., ... Mac, M. J. (2009). _Ecological requirements for pallid sturgeon reproduction and recruitment in the Lower Missouri River: A research synthesis 2005-08._ U.S. Geological Survey Scientific Investigations Report 2009–5201. Retrieved from https://pubs.er.usgs.gov/publication/sir20095201

DeLonay, A. J., Papoulias, D. M., Wildhaber, M. L., Annis, M. L., Bryan, J. L., Griffith, S. A., ... Tillitt, D. E. (2007). Use of behavioral and physiological indicators to evaluate _Scaphirhynchus_ sturgeon spawning success. _Journal of Applied Ichthyology_, _23_(4), 428–435. https://doi.org/10.1111/j.1439-0426.2007.00894.x

Detlaff, T. A., Ginsburg, A. S., & Schmallhausen, O. I. (1993). Environmental conditions of spawning and development. In G. G. Gause, & S. G. Vassetzky (Eds.), _Sturgeon fishes developmental biology and aquaculture._ Berlin, Germany: Springer-Verlag, 300 pp.

Dryer, M. P., & Sandvol, A. J. (1993). _Recovery Plan for the Pallid Sturgeon (Scaphirhynchus albus)._ Bismark, ND: U.S. Fish and Wildlife Service.

Du, H., Wei, Q. W., Zhang, H., Liu, Z., Wang, C., & Li, Y. (2011). Bottom substrate attributes relative to bedform morphology of spawning site of Chinese sturgeon _Acipenser sinensis_ below the Gezhouba dam. _Journal of Applied Ichthyology_, _27_(2), 257–262. https://doi.org/10.1111/j.1439-0426.2010.01660.x

Elliott, C. M., & Jacobson, R. B. (2016). Measurement of bedform migration rates on the Lower Missouri River in Missouri, USA using repeat measurements with a multibeam echosounder. In G. Constantinescu, M. Garcia, & D. Hanes (Eds.), _River Flow 2016_ (pp. 1536–1542). London: Taylor and Francis Group.

Elliott, C. M., Jacobson, R. B., & DeLonay, A. J. (2004). _Physical aquatic habitat assessment, Fort Randall segment of the Missouri River, Nebraska and South Dakota._ U.S. Geological Survey Open-File Report 2004–1060. doi: 10.3133/ofr20041060.

Erwin, S. O., Jacobson, R. B., & Elliott, C. M. (2017). Quantifying habitat benefits of channel reconfigurations on a highly regulated river system, Lower Missouri River, USA. _Ecological Engineering_, _103_, 59–75. https://doi.org/10.1016/j.ecoleng.2017.03.004

Ferrell, J. (1995). _Soundings: 100 years of the Missouri River navigation project._ Kansas City, KS: U.S. Army Corps of Engineers. Retrieved from https://apps.dtic.mil/dtic/tr/fulltext/u2/a322235.pdf

Fischenich, J. C., Buenau, K. E., Bonneau, J. L., Fleming, C. A., Marmorek, D. R., Nelitz, M. A., ... Gemeinhardt, T. R. (2018). _Science and Adaptive Management Plan Appendices and Attachments (ERDC/EL TR-18-XX)._ Retrieved from http://www.nwo.usace.army.mil/mrrp/mgmt-plan/

Fischenich, J. C., Marmorek, D. R., Nelitz, M. A., Murray, C. L., Ma, B. O., Buenau, K. E., ... Schwarz, C. J. (2018). *Science and Adaptive Management Plan (ERDC/EL TR-18-XX)*.

Funk, J. L., & Robinson, J. W. (1974). *Changes in the channel of the lower Missouri River and effects on fish and wildlife*. Jefferson City, MO: Missouri Department of Conservation Aquatic Series 11.

Gaeuman, D., & Jacobson, R. B. (2005). *Aquatic habitat mapping with an acoustic Doppler current profiler: Considerations for data quality*. U.S. Geological Survey Open-File Report 2005-1163. Retrieved from http://pubs.er.usgs.gov/publication/ofr20051163

Galat, D. L., & Lipkin, R. (2000). Restoring ecological integrity of great rivers: Historical hydrographs aid in defining reference conditions for the Missouri River. *Hydrobiologia*, *422*, 29–48. https://doi.org/10.1023/A:1017052319056

Hallberg, G. R., Harbaugh, J. M., & Witinok, P. M. (1979). *Changes in the channel area of the Missouri River in Iowa, 1879-1976*. Iowa Geological Survey Special Report Series Number 1 p. 32.

Haxton, T. J., & Cano, T. M. (2016). A global perspective of fragmentation on a declining taxon—The sturgeon (Acipenseriformes). *Endangered Species Research*, *31*, 203–210. https://doi.org/10.3354/esr00767

Jacobson, R. B., Annis, M. L., Colvin, M. E., James, D. A., Welker, T. L., & Parsley, M. J. (2016). *Missouri River Scaphirhynchus albus (pallid sturgeon) effects analysis—Integrative report 2016*. U.S. Geological Survey Open File Report 2016–5064. doi: 10.3133/sir20165064.

Jacobson, R. B., & Galat, D. L. (2006). Flow and form in rehabilitation of large-river ecosystems: An example from the Lower Missouri River. *Geomorphology*, *77*(3–4), 249–269. https://doi.org/10.1016/j.geomorph.2006.01.014

Jacobson, R. B., & Galat, D. L. (2008). Design of a naturalized flow regime-an example from the Lower Missouri River, U.S.A. *Ecohydrology*, *1*(2), 81–104. https://doi.org/10.1002/eco.9

Jacobson, R. B., Parsley, M. J., Annis, M. L., Colvin, M. E., Welker, T. L., & James, D. A. (2016). *Development of working hypotheses linking management of the Missouri River to population dynamics of Scaphirhynchus albus (pallid sturgeon)*. U.S. Geological Survey Open-file Report 2015–1236).

Jordan, G. R., Heist, E. J., Braaten, P. J., DeLonay, A. J., Hartfield, P., Herzog, D. P., ... Webb, M. A. H. (2016). Status of knowledge of the pallid sturgeon (*Scaphirhynchus albus* Forbes and Richardson, 1905). *Journal of Applied Ichthyology*, *32*(Supplement S1), 191–207. https://doi.org/10.1111/jai.13239

Jordan, G. R., Heist, E. J., Kuhajda, B. R., Moyer, G. R., Hartfield, P., & Piteo, M. S. (2019). Morphological identification overestimates the number of pallid sturgeon in the Lower Mississippi River due to extensive introgressive hybridization. *Transactions of the American Fisheries Society*, *148*(5), 1004–1023. https://doi.org/10.1002/tafs.10194

Kallemeyn, L. (1983). Status of the pallid sturgeon, *Scaphirhynchus albus*. *Fisheries*, *8*(1), 1–9.

Kock, T. J., Congleton, J. L., & Anders, P. J. (2006). Effects of sediment cover on survival and development of white sturgeon embryos. *North American Journal of Fisheries Management*, *26*, 134–141. https://doi.org/10.1577/M05-073.1

Krykhtin, M. L., & Svirskii, V. G. (1997). Endemic sturgeons of the Amur River: Kaluga, *Huso dauricus*, and Amur sturgeon *Acipenser Schrenckii*. *Environmental Biology of Fishes*, *48*(1–4), 231–240.

Laustrup, M. S., Jacobson, R. B., & Simpkins, D. G. (2007). *Distribution of potential spawning habitat for sturgeon in the Lower Missouri River, 2003–06*. U.S. Geological Survey Open-File Report 2007–1192.

Lundblad, E. R., Wright, D. J., Miller, J., Larkin, E. M., Rinehart, R., Naar, D. F., ... Battista, T. (2006). A benthic terrain classification scheme for American Samoa. *Marine Geodesy*, *29*(2), 89–111. https://doi.org/10.1080/01490410600738021

Manly, B. F. J., McDonald, L. L., Thomas, D. L., McDonald, T. L., & Erickson, W. P. (2002). *Resource selection by animals — Statistical design and analysis for field studies* (2 ed.). Dordrecdt, the Netherlands: Kluwer Academic Publishers.

Mayden, R. L., & Kuhajda, B. R. (1997). Threatened fishes of the world: *Scaphirhynchus albus* (Forbes & Richardson, 1905) (Acipenseridae). *Environmental Biology of Fishes*, *48*, 420–421.

McAdam, S. O., Crossman, J. A., Williamson, C., St-Onge, I., Dion, R., Manny, B. A., & Gessner, J. (2018). If you build it, will they come? Spawning habitat remediation for sturgeon. *Journal of Applied Ichthyology*, *34*, 258–278. https://doi.org/10.1111/jai.13566

McElroy, B., DeLonay, A. J., & Jacobson, R. B. (2012). Optimum swimming pathways of fish spawning migration in rivers. *Ecology*, *93*(1), 29–34. https://doi.org/10.1890/11-1082.1

Paragamian, V. L. (2012). Kootenai River white sturgeon: Synthesis of two decades of research. *Endangered Species Research*, *17*(2), 157–167. https://doi.org/10.3354/esr00407

Parsley, M. J., Beckman, L. G., & McCabe, G. T. Jr (1993). Spawning and rearing habitat use by white sturgeon in the Columbia River downstream from McNary Dam. *Transactions of the American Fisheries Society*, *122*, 217–227.

Reuter, J. M., Jacobson, R. B., Elliott, C. M., & DeLonay, A. (2009). *Assessment of Lower Missouri River physical aquatic habitat and its use by adult sturgeon (Genus Scaphirhynchus), 2005–07*. U.S. Geological Scientific Investigations Report 2009–5121.

Reuter, J. M., Jacobson, R. B., Elliott, C. M., Johnson, H. E. III, & Delonay, A. J. (2008). *Hydraulic and substrate maps of reaches used by sturgeon (Genus Scaphirhynchus) in the Lower Missouri River, 2005-07*. U.S. Geological Survey Data Series 386.

Rochard, E., Castelnaud, G., & Lepage, M. (1990). Sturgeons (Pisces: Acipenseridae); threats and prospects. *Journal of Fish Biology*, *37*(sA), 123–132. https://doi.org/10.1111/j.1095-8649.1990.tb05028.x

Smith, A., Smokorowski, K. E., & Power, M. (2017). Spawning lake sturgeon (*Acipenser fulvescens Rafinesque*, 1817) and their habitat characteristics in Rainy River, Ontario and Minnesota. *Journal of Applied Ichthyology*, *33*(3), 328–337. https://doi.org/10.1111/jai.13372

Steffensen, K. D., Chojnacki, K. A., Kalie, J. A., Bartron, M. L., Heist, E. J., Winders, K. R., ... Welker, T. L. (2019). Evidence of limited recruitment of pallid sturgeon in the Lower Missouri River. *Journal of Fish and Wildlife Management*, https://doi.org/10.3996/022018-JFWM-013

Sulak, K. J., & Clugston, J. P. (1998). Early life history stages of Gulf sturgeon in the Suwannee River, Florida. *Transactions of the American Fisheries Society*, *127*(5), 758–771. https://doi.org/10.1577/1548-8659(1998)127<0758:ELHSOG>2.0.CO;2

USFWS (United States Fish and Wildlife Service) (1990). *Endangered and threatened wildlife and plants; determination of endangered status for the pallid sturgeon (5O CFR Part 17)*. U.S. Fish and Wildlife Sercvice. Retrieved from http://digitalcommons.unl.edu/cgi/viewcontent.cgi?article=1033&context=endangeredspeciesbull

USFWS (United States Fish and Wildlife Service) (2014). *Revised recovery plan for the pallid sturgeon (Scaphirhynchus albus)*. Denver, CO: U.S. Fish and Wildlife Service.

Wang, Y., Xia, Z., & Wang, D. (2012). Characterization of hydraulic suitability of Chinese sturgeon (*Acipenser sinensis*) spawning habitat in the Yangtze River. *Hydrological Processes*, *26*(23), 3489–3498.

Weiss, A. D. (2001). *Topographic positions and landforms analysis [abs]*. San Diego, CA. Paper presented at the ESRI International User Conference.

Wildhaber, M. L., DeLonay, A. J., Papoulias, D. M., Galat, D. L., Jacobson, R. B., Simpkins, D. G., & Mac, M. J. (2007). *A conceptual life-history model for pallid and shovelnose sturgeon*. U.S. Geological Survey Circular

1315. Retrieved from https://pubs.usgs.gov/circ/2007/1315/pdf/circ_1315.pdf

Wyman, M. T., Thomas, M. J., McDonald, R. R., Hearn, A. R., Battleson, R. D., Chapman, E. D., ... Klimley, A. P. (2017). Fine-scale habitat preference of green sturgeon (*Acipenser medirostris*) within three spawning locations in the Sacramento River California. *Canadian Journal of Fisheries and Aquatic Sciences*, *75*(5), 779–791. https://doi.org/10.1139/cjfas-2017-0072