

[Southeastern Fishes Council Proceedings](https://trace.tennessee.edu/sfcproceedings)

[Volume 1](https://trace.tennessee.edu/sfcproceedings/vol1) | [Number 64](https://trace.tennessee.edu/sfcproceedings/vol1/iss64) Article 3

May 2024

Spawning Ecology and Spawning Site Fidelity of Alligator Gar, Atractosteus spatula, in the Fourche LaFave River: Implications for River-Floodplain Management and Alligator Gar Conservation

S. Reid Adams Department of Biology, University of Central Arkansas, radams@uca.edu

Thomas E. Inebnit United States Fish and Wildlife Service, Conway Field Office, thomas_inebnit@fws.gov

Lindsey C. Lewis United States Fish and Wildlife Service, Conway Field Office, lindsey_lewis@fws.gov

Christopher J. Naus Department of Biology, University of Central Arkansas, nauscj@gmail.com

Edward Kluender Colorado State University, erkluender@gmail.com

Follow this and additional works at: [https://trace.tennessee.edu/sfcproceedings](https://trace.tennessee.edu/sfcproceedings?utm_source=trace.tennessee.edu%2Fsfcproceedings%2Fvol1%2Fiss64%2F3&utm_medium=PDF&utm_campaign=PDFCoverPages)

C Rattopage for additional authors of the [Terrestrial and Aquatic Ecology Commons](https://network.bepress.com/hgg/discipline/20?utm_source=trace.tennessee.edu%2Fsfcproceedings%2Fvol1%2Fiss64%2F3&utm_medium=PDF&utm_campaign=PDFCoverPages)

Recommended Citation

Adams, S. Reid; Inebnit, Thomas E.; Lewis, Lindsey C.; Naus, Christopher J.; Kluender, Edward; and Spooner, Geoffry G. (2024) "Spawning Ecology and Spawning Site Fidelity of Alligator Gar, Atractosteus spatula, in the Fourche LaFave River: Implications for River-Floodplain Management and Alligator Gar Conservation," Southeastern Fishes Council Proceedings: No. 64.

Available at: [https://trace.tennessee.edu/sfcproceedings/vol1/iss64/3](https://trace.tennessee.edu/sfcproceedings/vol1/iss64/3?utm_source=trace.tennessee.edu%2Fsfcproceedings%2Fvol1%2Fiss64%2F3&utm_medium=PDF&utm_campaign=PDFCoverPages)

This article is brought to you freely and openly by Volunteer, Open-access, Library-hosted Journals (VOL Journals), published in partnership with The University of Tennessee (UT) University Libraries. This article has been accepted for inclusion in Southeastern Fishes Council Proceedings by an authorized editor. For more information, please visit <https://trace.tennessee.edu/sfcproceedings>.

Spawning Ecology and Spawning Site Fidelity of Alligator Gar, Atractosteus spatula, in the Fourche LaFave River: Implications for River-Floodplain Management and Alligator Gar Conservation

Abstract

We studied the spawning ecology of Alligator Gar, Atractosteus spatula, in the Fourche LaFave River (FLR) of Arkansas to better understand their reproductive ecology and spawning resource requirements. Evidence of spawning was only observed in floodplain tributary habitats, particularly the small, adventitious headwater stream West Fork Mill Creek (WFMC). A mid-May to mid-June spawning season was observed for Alligator Gar in the FLR that corresponded with rising water levels (mostly due to backflooding from the Arkansas River) and increased water temperatures (> 20°C). Direct spawning observations at WFMC were made on 17 June 2007, 15 June 2008, 23 May 2010, and 3 June 2013. Continued use of the same site indicates high spawning site fidelity. General spawning behavior was typical of gars consisting of circular swimming paths by groups, a lead individual (presumably a female) followed by males, and thrashing of shallow water as gametes were emitted. Eggs were mostly attached to herbaceous wetland vegetation, in particular Carex sp., at WFMC despite the presence of inundated shrubs, small trees, and nearby cropland during all years. Alligator Gar laid eggs in shallow water, often only 14 cm or less from the surface, and early larval stages were mostly sedentary, needing \sim 8 days post spawn to reach a more active developmental stage. Eggs and larvae were highly vulnerable to lowering water levels, and we observed desiccation of eggs in some years. Floodplain tributaries functioned as both movement corridors and spawning and nursery habitat for Alligator Gar in the FLR riverscape. Maintaining passage within corridors connecting adult staging and spawning/rearing habitats is important for conservation. As an obligate spawner in open canopied, early successional floodplain habitats, Alligator Gar should be a focal species to ensure conservation programs include floodplain fish conservation, habitat heterogeneity, and availability of herbaceous wetland vegetation in their conservation objectives and goals rather than focusing merely on reforestation.

Keywords

Wetland Vegetation, Carex, Floodplain Tributary, Floodplain Restoration

Creative Commons License

This work is licensed under a [Creative Commons Attribution-No Derivative Works 4.0 International](https://creativecommons.org/licenses/by-nd/4.0/) [License](https://creativecommons.org/licenses/by-nd/4.0/).

Cover Page Footnote

Resources to conduct this research were provided by the Department of Biology at the University of Central Arkansas (UCA) and the Conway Field Office of the United States Fish and Wildlife Service. Partial funding was provided during 2009 and 2010 from State Wildlife Grant funds administered by the Arkansas Game and Fish Commission (AGFC). We thank the private landowners for allowing us access to study sites. J.P. Atkinson provided invaluable help throughout many aspects of this project. Numerous students from UCA contributed to data collection over the study period. Dr. Rick Noyes (UCA) helped with moistsoil plant identification, and George Gavrielides helped with land use/land cover analyses. Dr. Ginny Adams (UCA) provided underwater photos of larvae and provided comments on an earlier draft. We thank Eric Brinkman (AGFC) for providing valuable comments on an earlier draft.

Authors

S. Reid Adams, Thomas E. Inebnit, Lindsey C. Lewis, Christopher J. Naus, Edward Kluender, and Geoffry G.

Spooner

INTRODUCTION

Alligator Gar (*Atractosteus spatula*) has declined relative to its historic range (Etnier and Starnes 1993; Robison and Buchanan 2020), although existing populations in Texas, Oklahoma, Arkansas, Louisiana, and Alabama have been relatively stable over recent years (Smith et al. 2020). Decline in Alligator Gar populations and overall range has been multifaceted with overexploitation, eradication efforts, barriers, pollutants, and water quality changes having all likely contributed (Burr 1931; Scarnecchia 1992; Etnier and Starnes 1993; Mendoza et al. 2002; O'Connell et al. 2007; Brinkman and Fisher 2020; Jelks et al. 2008; Mendoza-Alfaro et al. 2008; Inebnit 2009; Gonzalez et al. 2015; Lochmann et al. 2021). However, habitat alteration (e.g., alteration and replacement of native wetland vegetation) and inaccessibility, along with hydroperiod alteration (e.g., deviation from and de-coupling of flood-pulse frequency, timing, and duration from reproductive cycles) have been considered primary factors for declines since they directly impede reproductive success (Ferrara 2001; Buckmeier et al. 2017; Kluender et al. 2017; van der Most et al. 2018). Collection of detailed reproductive ecology data is paramount to our understanding of the complex interaction between floodplain habitat connectivity and reproductive success of river-floodplain fishes, such as Alligator Gar, particularly within context of the altered ecosystems within which they exist (*sensu* King et al. 2003).

Limited data exist on spawning, early life history, and ecological factors influencing recruitment of Alligator Gar, particularly relative to other fishes (Smith et al. 2020). Few direct observations of spawning have been made, and they mostly described groups of several fish thrashing in shallow water with broadcasted eggs adhering to nearby structure, usually aquatic vegetation (Cook 1959; Inebnit 2009; K. Kimmel 2014 personal communication; Brinkman and Fisher 2020). Spawning usually occurs in association with flooding during spring/ early summer when water temperatures generally exceed 20°C (Suttkus 1963; Allen et al. 2014; Echelle and Grande 2014; Snow and Long 2015; Buckmeier et al. 2017). Larvae hatch within 72 hours, adhere to structure with an adhesive gland for a few days surviving on yolk reserves, becoming freeswimming and exogenously feeding soon thereafter (Aguilera et al. 2002; Mendoza et al. 2008; Inebnit 2009; Echelle and Grande 2014). Growth of wild Age-0 Alligator Gar is rapid, averaging 3.6 to 5.13 mm/day across Texas populations studied (Sakaris et al. 2019). Recruitment success is coupled with magnitude and timing of flooding, with recruitment found to be greatest when floods occur during the spawning season and floodplain habitats remain inundated allowing for development of early life stages (Inebnit 2009; Buckmeier et al. 2017; Robertson et al. 2018). A general framework exists for understanding reproduction of Alligator Gar, but additional details of spawning (e.g., conditions, timing, location, and vegetation characteristics) and *in situ* early life history (e.g., hatching and development) would aid understanding of limitations to Alligator Gar reproductive success.

Alligator Gar is a Species of Greatest Conservation Need in Arkansas where it is mostly known from the largest rivers in the state (e.g., Arkansas, Ouachita, Red, and White rivers) (Robison and Buchanan 2020) (Figure 1). There were no records of Alligator Gar in the Fourche LaFave River (FLR), a major tributary of the Arkansas River, prior to 1987 (Robison and Buchanan 2020); however, this population was known to local landowners and fishers. The lower segment of the FLR is relatively unique in that it has a connected, unleveed floodplain and a sinuous main channel with varying depths, high amounts of in-channel wood, and a vegetated riparian zone (personal observation). Telemetry data indicate Alligator Gar individuals reside for much of the year in the FLR, but also regularly move between the FLR and adjacent Arkansas River (Kluender et al. 2017). The FLR population is distinctive in that it is one of the most upstream, extant populations of the Arkansas River, and is a population greatly utilizing a smaller, medium-sized river (Robison and Buchanan 2020).

We have been studying reproductive ecology of Alligator Gar in the Fourche LaFave River of Arkansas since 2007, and have collected data on multiple life stages (Inebnit 2009) (Figure 1). Our goal is to describe field details of spawning and egg/larva development in this modified riverscape where reproductive success still occurs. Direct field observations were made during 2007, 2008, 2010, and 2013. This study increases our knowledge and understanding of Alligator Gar reproductive ecology and resource requirements, particularly in modified rivers inland within the Mississippi River system where most populations of Alligator Gar have drastically declined or become extirpated (Etnier and Starnes 1993). Information from this field-based case study highlight the need to reconsider aspects of floodplain habitat management within the Mississippi River system to conserve Alligator Gar.

Figure 1. Alligator Gar (*Atractosteus spatula*) individuals collected in the Fourche LaFave River (FLR) watershed. (Top) – Adult (~ 182 cm total length) collected in the mainstem FLR on 5 December 2008. (Bottom left) – Young-ofyear individuals (10-25 cm total length) collected at night on 1 August 2007 in the mainstem FLR. (Bottom right) – Young-of-year (~ 7 cm total length) photographed *in situ* in shallow water (< 50 cm) on 17 June 2007 in West Fork Mill Creek.

METHODS

Study Area

The Fourche LaFave River (FLR) meets the Arkansas River near Bigelow, Arkansas (Figure 2). It is a medium-sized river (4 - 5th order) that begins from its headwaters near the Arkansas/Oklahoma border and flows east approximately 225 km through the Ouachita Mountains [see Naus and Adams (2018) for discharge data]. The main channel of the FLR has not been channelized and large woody debris abounds, characteristics somewhat unique for a lowland river in the southern United States. At the time of this study, much of the floodplain was composed of pasture or row-crop agriculture land. Our research spanned the lower approximately 50 river kilometers because this is where the floodplain was most extensive; however, most alligator gar telemetry detections during the spawning season (Kluender et al. 2017) and observations of spawning and early life history (in the current study) were in the lower 22 rkm. Land use/land cover (LULC) was approximated for the floodplain corridor of the lower 22 rkm using aerial imagery of flood extent of the 2019 flood in combination with the National Land Cover Data Base (NLCD), and LULC was as follows: cultivated crops 35.7%, pasture/hay 34.7%, woody wetlands 11.0%, forest 9.8 %, developed 3.6%, open water 2.8 %, all other categories ≤ 1.0 % (NLCD) 2019). Some floodplain alterations such as the construction of ditches, culverts, and water retention ponds have occurred, but the floodplain remains unleveed and contains multiple tributary (approximately 40) and oxbow (approximately 18) habitats. The FLR is regulated by one mainstem impoundment (Nimrod Dam) that forms Nimrod Lake approximately 100 km upstream of the confluence with the Arkansas River. However, the Arkansas River and its lock and dam system also play an important role in the hydrology of the lower FLR, which flows into Pool 7 of the Arkansas River. Inundation of the FLR floodplain is typically associated with high discharge in the Arkansas River resulting in "back flooding" of the FLR and pushing of water onto the floodplain.

Most of our successful spawning and nursery observations were made associated with a first to second order lowland headwater stream of the Mill Creek tributary known as West Fork Mill Creek (WFMC) (Figure 2). High discharge/stage on the mainstem FLR pushes or backflows water up Mill Creek (against typical flow direction) causing WFMC to flood outside its banks. The site on WFMC is approximately 2.7 rkm from the mainstem FLR. Preceding spawning, adults have a tendency to stage near the confluence of Mill Creek and other tributaries of the FLR (Kluender et al. 2017). Adults ascend Mill Creek, swim into WFMC, and spawn in associated, flooded vegetation in the immediate floodplain area (Inebnit 2009; Kluender et al. 2017). To reach the WFMC spawning area, adults must pass a county road by swimming through culverts or over the road, depending on water levels. During non-flooded conditions WFMC was about 10 m wide and 0.7 m deep in the general spawning area upstream of the county road. All land in the Mill Creek watershed, including WFMC, was privately owned during our study. Specific land use of the study area was row-crop agriculture prior to 2004, and then it was entered into the Conservation Reserve Program (USDA) and bottomland hardwood trees were planted. The primary spawning area was classified as woody wetlands with intermixed emergent herbaceous wetlands (NLCD 2019). Total area of herbaceous wetland vegetation was about 48 hectares in the general study area. This patch of non-cultivated herbaceous vegetation was set within a local landscape matrix of mostly row-crop agriculture and pasture. Approximately 220 hectares of active row-crop agriculture existed directly between the FLR and WFMC study area.

Figure 2. Map of the lower Fourche LaFave River and primary study site in West Fork Mill Creek in central Arkansas. Other lowland, headwater streams opportunistically monitored throughout the study period are indicated. The inset map shows the Fourche LaFave River (shaded), and the star illustrates location of the general study area.

The WFMC study area is mostly an open canopy habitat having a diversity of vegetation types for potential spawning and egg and larval attachment. During the spawning period of all years (May through June), patches of common buttonbush (*Cephalanthus occidentalis*), swamp privet (*Foresteira acuminate*), and rosemallows (*Hibiscus* sp.) were present along the edges of WFMC, edges of ephemeral side channels, and sparsely distributed in the general floodplain area. Small bald cypress (*Taxodium distichum*), oaks (*Quercus* spp.), and other lowland hardwoods (generally < 3 m) were sparsely distributed across slightly higher elevations during all years, but their density and size has increased over time. These higher elevations were historically used for row-crop agriculture. Herbaceous wetland vegetation, including *Carex* spp., *Polygonum* sp., *Ludwigia* sp. and others, occurred from the stream edge across lower elevations of the general floodplain area at WFMC, including within ephemeral side channels maintained by beavers (*Castor canadensis*). Moderate to high amounts of wetland vegetation covered lower elevations of the site during the spawning period of all years except during 2008, when extensive flooding occurred at the site beginning mid-March (Figure 3) that substantially impeded/delayed above ground plant growth that year and caused the almost complete decay of dormant herbaceous vegetation from the previous year. Inundated limbs of shrubs and herbaceous wetland vegetation were present as potential spawning sites at low to moderate stages of flooding at WFMC. At higher

flood stages, inundated shrubs, small trees, and some (though sparse) herbaceous wetland vegetation were available for spawning along floodplain margins.

Sampling – Spawning, Eggs, and Larvae (2007, 2008, 2010, 2013)

We studied spatial and temporal aspects of Alligator Gar reproduction, within the lower 50 km of the FLR riverscape, by sampling larvae (< 32.5 mm TL) and early juveniles (32.5-70.0 mm TL) in the field and by making direct observations of spawning and subsequent egg and larval stages. Young gars tend to swim at the water's surface during the day (Echelle and Riggs 1972; Moore et al. 1973) facilitating the effectiveness of daytime visual searches and capture with dipnet or seine. Spawning adult gars are typically conspicuous in shallow water (Echelle and Grande 2014), and we visually searched for spawning aggregations during daytime hours. When spawning was observed, we attempted to collect ecological data on eggs and larvae in the field. Sampling occurred from April through June, since gar species generally spawn during these months at temperatures ranging from 20-30°C (Wallus et al. 1990; Echelle and Grand 2014). Spatially and temporally intensive sampling occurred during our sampling window in 2007 and 2008. The ultimate goal was to locate spawning and rearing sites of Alligator Gar in the FLR riverscape during these initial two years of the study (2007 and 2008). Locating early life stages *in situ* provided initial clues towards finding these important habitats and subsequently led to our ability to make direct spawning observations in subsequent years. Following 2008, we focused sampling of spawning, eggs, and larvae at the West Fork Mill Creek area, although we opportunistically sampled other tributaries based on what we learned during 2007 and 2008.

A spatial assessment of reproduction was accomplished during 2007 and 2008 by sampling in three *a priori* defined macro-habitat types representing a range of potential slack water spawning areas: main channel border (vegetated shallow-water habitat in immediate proximity to the river bank), adjacent floodplain (flooded areas adjacent to the main channel including flooded fields, floodplain ponds, oxbow lakes, etc.), and tributary backwater (channels, channel borders, and immediate flooded areas associated with first to second order floodplain tributaries). Sample sites were haphazardly selected based on having shallow depths, no water velocity, and presence of some type of vegetated structure (herbaceous and woody) to represent macro-habitat types and spanned approximately 50 km of the lower FLR. Our selection of sites could have resulted in bias, but it was likely negligible since we had no prior basis for selection of sites other than vegetation presence and location outside of the main channel (i.e., on the floodplain). Sites ($n = 36$ in 2007 and $n = 33$ in 2008) were visited by boat, kayak, or truck one to nine times during 2007 and one to 23 times during 2008, and habitats were spatially and temporally interspersed over the threemonth sampling period during both years. Differences in site visits were mostly due to ease of accessibility whereby sites that could be visited by kayak and truck were sampled more often. Increased visits (e.g., 23) were made to some sites during 2008 where Alligator Gar eggs and larvae were found during 2007. Fifteen minutes of visual searching (approximately 50 meters of shoreline) occurred at every site by a two-person crew. Visual searching consisted of wading along shallow shorelines or paddling by boat along deeper flooded channel borders. A seine (3.6m x 2.4m x 0.16cm) was used occasionally in shallow habitats clear of debris. When gar larvae were present, both *Atractosteus* and *Lepisosteus* spp. (mostly Shortnose Gar, *Lepisosteus platostomus*, and Spotted Gar, *Lepisosteus oculatus*), up to ten representative individuals were collected and fixed in 5% formalin for further analysis. The primary objective was to determine presence/absence of Alligator Gar larvae, but abundance was also quantified using a ranked scale:

(0 larvae = 0, 1-10 larvae = 1, 11-100 larvae = 2, >100 larvae = 3). *Lepisosteus* spp. larvae were collected to ensure positive identification from Alligator Gar larvae and for comparisons of abundance and habitat use with Alligator Gar.

Monitoring for spawning activity coincided with the larval spatial assessment during 2007 and 2008 as described previously. After 2008, sampling efforts for spawning activity were primarily focused on West Fork Mill Creek (WFMC), a floodplain tributary in the lower FLR, based on findings during 2007 and 2008. Frequency of visits to WFMC varied with flood frequency and magnitude. We typically started visiting the site 24 hrs. prior to water backflooding into the site based on river stage predictions and our knowledge of the study area, and continued monitoring daily until floods receded or continued high water rendered searches futile. Monitoring of the WFMC area entailed two to four researchers watching for activity at the road crossing, walking the flooded edge, and floating the area in kayaks. Search effort varied with level of flooding, but generally ranged from 3 to 6 hrs. Surveys at low to moderate flood levels encompassed \sim 1.0 km of shoreline and channel. We searched the entirety of flooded area during surveys up to ~ 0.5 km²; area searched ranged from ~ 0.1 km² at initial flooding up to ~ 0.5 km² during high levels of flooding. Descriptions of spawning activity were made from field notes and videos of spawn events. Following any observed spawns and apparent cessation of spawning activity, locations of egg clusters (loose aggregations) within the search area were marked with flagging and development monitored. Water depth was measured at the center of clusters with a meter stick. The primary substrate to which eggs were attached within each cluster was recorded. *Lepisosteus* spp. also spawned in this area and have relatively large-sized eggs similar to Alligator Gar; therefore, a subset of eggs from 2007, 2008, and 2013 were hatched in the laboratory for species verification when there was uncertainty. Following a spawn during 2013, we opportunistically sampled adults leaving the spawning site with gill nets to determine sizes of individuals that participated in the spawn and sex ratio. These important data do not exist from other Alligator Gar spawning observations based on our knowledge.

Eggs and subsequent larvae were monitored daily until eggs were desiccated or larvae were no longer observed. Attachment to substrate with cement organ was observed *in situ*. These behaviors provided information on stage-specific vulnerability to water level change. Presumably, increased free-swimming behavior and decreased propensity to attach to substrate increased chances of survival under conditions of lowering water levels post hatch. General developmental stages were recorded daily, with particularly attention given to absorption of yolk over time. Five to ten individuals per day were fixed in 5% formalin and measured with calipers (total length). Two spawns occurred at WFMC during 2007, the second of which we directly observed. Evidence of an earlier spawn was indicated by presence of early juveniles at WFMC prior to our direct observation. Spawn date of these individuals was estimated using size at capture and developmental parameters (i.e., size at hatch and daily growth rate) quantified by Mendoza et al. (2002) as described by Adams et al. (2006) and Inebnit (2009).

Point-in-time measurements of water temperature and dissolved oxygen were made with digital probes opportunistically in the FLR channel and corresponding with site visits to WFMC during most years. In addition, daily main channel FLR water temperatures were monitored during 2009 to 2013 with HOBO® Pro v2 data loggers (Onset, Bourne, Massachusetts) preceding and during the spawning season.

During the study period, particularly when conditions were most conducive to spawning and/or spawning was observed at WFMC, we opportunistically searched and monitored other tributaries, mainstem borders, oxbow lakes, and seasonally inundated floodplain habitats for eggs, larvae, and juveniles. Efforts in other habitats were more frequent during 2007, 2008, 2009, 2010, 2012, and 2015 corresponding with other research projects in the FLR system (e.g., Kluender et al. 2017; Naus and Adams 2018). Of particular interest was nearby Lawson Creek (Figure 2) where larvae and Age-0 juveniles were found during 2007 (Inebnit 2009). We found shed radio transmitters (from the Kluender et al. 2017 study) previously attached to adult Alligator Gar in the Rankin Creek system during a flood on May 14, 2009 associated with large, recently desiccated eggs that likely represented a failed spawn attempt. Following flooding during 2015, we collected 4 Age-0 Alligator Gar in Lawson Creek and 1 Age-0 individual in the Rankin Creek system. Inability to locate other substantial spawning and recruitment sites in the FLR further led to focusing most efforts on WFMC.

RESULTS

Spatial Assessment of Larvae and Early Juveniles

From 26 April to 29 June 2007, 38 different sites across three macrohabitats (10 tributary backwaters, 5 adjacent floodplain, and 23 main channel border) were sampled during 28 sampling trips resulting in 71 total samples. Young-of-year (YOY) *Lepisosteus* spp. (larvae and early juveniles) were collected beginning 16 May and occurred at 17 of the 38 (45%) sites throughout the season and in all three macrohabitats. Conversely, Alligator Gar YOY were found in only two of the 38 (5%) sites (WFMC and Lawson Creek) during 2007, representing only the tributary backwater macrohabitat. In 2007 YOY Alligator Gar were found at WFMC on five sampling trips from 5 June to 20 June [larvae: > 1000 (8.1-12.3 mm TL); early juvenile: 47 (48.0-67.0 mm TL]. Capture of early juvenile Alligator Gar on 5 June and 7 June indicated spawning occurred prior to 17 June (see "Field Descriptions of Spawning"). We estimated these fish 48-67 mm TL were 15- 18 days old and spawned around 19 May. At Lawson Creek, YOY Alligator Gar were found on 22 June and 29 June $\lceil \text{larvae:} \rangle$ 100 (13.1-16.8 mm TL); early juvenile: 1 (47.6 mm TL)]. Youngof-year of both *Lepisosteus* spp. and Alligator Gar were collected when floodplain water temperatures ranged from 25-30°C. Despite the presence of *Lepisosteus* spp. larvae at each habitat type, rank abundances of all Lepisosteidae larvae and early juveniles were highest on average in tributary backwaters (1.38 \pm 0.38 SE) and tended to be lower in adjacent floodplains (0.80 \pm 0.58 SE) and main channel borders $(0.65 \pm 0.21$ SE).

From 22 April to 21 July 2008, 35 different sites (10 tributary backwaters, 5 adjacent floodplain, and 20 main channel border) were sampled during 34 trips to the FLR resulting in 123 samples. *Lepisosteus* spp. YOY were found beginning on the first day of sampling (22 April 2008), but were collected at fewer sites relative to 2007 (11 of 35 sites) and at all three macrohabitat types. Alligator Gar YOY were not found during the 2008 sampling season, but one observation of spawning was made in a tributary backwater (WFMC) on 15 June (see below). *Lepisosteus* spp. YOY were collected when floodplain water temperatures were 22-31°C. Rank abundances of *Lepisosteus* spp. larvae and early juveniles tended to be highest in tributary backwaters (1.00 ± 1.00) 0.46 SE) and generally lower in adjacent floodplains $(0.60 \pm 0.40 \text{ SE})$ and main channel borders $(0.25 \pm 0.10 \text{ SE})$.

Figure 3. Daily mean stage (lines) of the Fourche LaFave River at Houston, Arkansas (USGS 07263115) (See Figure 2) and water temperature (points) in the main channel near the confluence of West Fork Mill Creek from March to September during Alligator Gar spawning years. The horizontal line at a stage of 6.4 m indicates approximate stage that water flows upstream of the road crossing and flooding begins at the West Fork Mill Creek study site. The inverted triangles denote days of spawning. Spawning was not directly observed in mid May of 2007 but inferred from the collection of early juveniles.

Field Descriptions of Spawning

Direct observations of Alligator Gar spawning during the initial two years of study (2007 and 2008) included relatively few adult individuals. We observed gar spawning at WFMC during 17 June 2007 from 1300 to 1535 hours at 27.5°C, a temperature 1.25°C warmer than mainstem FLR (Figure 3). A bowfisher communicated he had observed spawning at the same location earlier that day (approximately 0900 hours). Observations of spawning were made again during 15 June 2008; the site was monitored from 0600 to approximately 1700 hours, but spawning was only observed from 0600 to 0930 at 29.5 °C, ~ 1.8 °C warmer than the FLR. Spawning during 2008 occurred approximately 450 m downstream from the spawn event observed during 2007. Number of adults present during both years was estimated to be between four and seven based on observed spawning bouts and surface breaches (porpoises). Spawning bouts consisted of a group of two to four individuals thrashing, for only a few seconds, in less than 1 m of water and in proximity of inundated wetland vegetation (*Carex* sp.) or shrub (e.g., *Forestiera acuminate*, *Cephalanthus occidentalis*, and *Hibiscus* sp.). Groups of fish were observed swimming together and making

passes repeatedly in the same area. These swimming passes consisted of making a circle through deeper water and eventually coming back to the same shallow area to begin another spawning bout. Bouts of spawning during both years were verified the next day by presence of Alligator Gar eggs. A subset of eggs from 2007 and 2008 were hatched in the laboratory for species verification. Spawning and eggs were never observed at nearby Lawson Creek. However, observations were made of adult Alligator Gar actively porpoising in Lawson Creek from 28 May to 30 May 2008 and from 10 June to 11 June 2008, with water temperatures ranging from 23-30°C. These dates corresponded with increases in river level of the lower FLR (Figure 3). These adult gars appeared to remain in this tributary until water levels began to descend, which seemed to cause an immediate evacuation out of the backwater area due to the lack of observed porpoising activity.

Alligator Gar were observed spawning at WFMC during the morning of 23 May 2010 in the primary spawning area near the 2007 location (Figure 2). Water levels had crested overnight, and water was flowing out of the spawning area back to the Fourche LaFave River when we arrived that morning (Figure 3). Bouts of spawning were observed from 0639 to 0930 hours when water temperature was 23.1° C at WFMC and slightly cooler than the mainstem FLR at 23.4° C. A group of 10 or fewer adults was spawning in an expanse of herbaceous wetland plants (mostly *Carex lupulina*, Hop Sedge) devoid of woody vegetation. There appeared to be multiple large individuals (likely females) that were joined by smaller individuals (probably males) and spawning would occur as previously described. Spawning ceased by 0930 hours, and adults were observed leaving the area and crossing the flooded road soon thereafter. During this event, two of the observed individuals were fish previously captured and tagged with radiotelemetry transmitters as part of an in-progress movement and habitat use study (Kluender et al. 2017). Both tagged adults (total lengths of 1.69 and 2.13 m) left the spawning area by 1345 hours, and no other adults were observed.

Direct observations of spawning were again made at WFMC during the morning of 3 June 2013 (Figure 3). Spawning occurred very near (< 50 m) the same location we found most of the eggs during 2007 and 2010 and involved more adults than previous years. The day prior to spawning, 2 June, we visited the site from 0730 to 1200 hours and observed no spawning activity. Water was backflowing from the Fourche LaFave River through the culverts at a flow rate of 0.17 to 0.25 m/s (19.8 to 20.0°C), and depth of water within culverts was 0.91 m. Approximately 10 small adults and one large adult Alligator Gar were observed downstream of the culverts. We visited the site on 3 June from 0700 to 1800 hours. Water levels rose throughout the night and water was continuing to back flow through the culverts and over the road at 0700. Seven bouts of spawning were observed from 0700 to 0900 hours (22.2 to 23.5 °C) by two distinct groups of fish (\sim 8 to 15 individuals each) at temperatures \sim 1.5°C warmer than the main channel of the FLR. Larger individuals led groups followed by smaller fish. Groups swam just under the water's surface, and tended to make wide circles within an area of mostly flooded herbaceous wetland vegetation with sparse shrubs/small trees (Figure 4A). During bouts of spawning, vigorous thrashing would begin at the front of the group and then joined by the smaller individuals; bouts would last 5 to 10 seconds. No spawning activity was observed after 0900 hours. Backflow into the floodplain area ceased by approximately 1100 hours, and water was flowing back to the Fourche LaFave River by 1115 hours; from 1300 to 1700 hours, outflow rate ranged from 0.13 to 0.28 cm/s.

We attempted to collect adults, presumably leaving the spawning area, from 1100 to 1700 hours with two gill nets (45.7 m X 3.0 m; 7.6 and 12.7 cm mesh) set just upstream of the culverts on 3 June 2013. Captured fish were measured (total length and body girth with a fiberglass tape to nearest 0.01 m), weighed (nearest 1.0 kg with hanging scales), and released downstream of the road crossing. We tried to determine sex on most individuals by applying pressure to the abdominal area to express gametes, and examined the urogenital opening for swelling.

Figure 4. Adult Alligator Gar preparing to spawn in herbaceous wetland vegetation during 2013 at the study site in the Fourche LaFave River system (A). Yolk-sac stage Alligator Gar larva attached to a leaf blade of *Carex lupulina* (Hop Sedge) using its adhesive organ during 2007 (B) (photo taken *in situ* by Ginny Adams). Yolk-sac larvae attached to submerged debris during 2007 (C) (photo taken *in situ* Ginny Adams). Spawning site 24 hours after spawning during 2010 (D).

Eggs were desiccated as a result of falling water levels. The vegetated, ephemeral ditch commonly used by Alligator Gar for spawning is on the right-hand side of the photo.

In total, we captured 13 Alligator Gar ranging in total length from 1.19 to 2.15 m on 3 June 2013 (Table 1). The first fish was captured at 1125 hours, and the last fish was captured at 1651 hours. At least two fish were entangled but could not be landed. Five captured individuals readily expressed milt as soon as pressure was applied (mean total length 133 cm). Gametes could not be expressed from four individuals, and these fish had notably swollen urogenital areas. These probable females had a mean length of 1.75 m (Table 1). We observed no adult Alligator Gar upstream of the culverts after 1700 hours on 3 June 2013 or on subsequent days.

Total Length (m)	Weight (kg)	Girth (cm)	Sex
1.36	16.0	56.0	Not Determined ^a
1.42	17.0	56.0	Not Determined ^a
1.34	14.0	54.0	Not Determined ^a
1.92	47.0	80.0	Probable Female ^b
1.74	14.0	54.0	Probable Female ^b
1.21	10.0	50.0	Not Determined ^a
1.63	28.0	66.0	Male ^c
2.15	64.0	88.0	Probable Female ^b
1.27	13.0	53.0	Male ^c
1.25	11.0	50.0	Male ^c
1.19	8.0	44.0	Probable Female ^b
1.28	12.0	52.0	Male ^c
1.24	10.0	46.0	Male ^c

Table 1. Characteristics of thirteen adult Alligator Gar captured with gill nets exiting the spawning location at West Fork Mill Creek on 3 June 2013.

 \sqrt{a} We did not try to express gametes from these individuals

 b Milt was not expressed from these individuals and they had swollen urogenital openings</sup>

^cMilt was easily expressed during palpation of the abdomen

Field Descriptions of Eggs and Larvae

Following the 17 June 2007 spawn event at WFMC, Alligator Gar eggs were observed in eight distinctly separate clusters/aggregations (20-50 cm diameter) within an area of approximately 15 m² (Table 2). Eggs were mostly adhered to recently flooded wetland vegetation (*Carex lupulina*), and a small percentage were attached to floating woody debris. The majority of eggs were found in the upper half of the water column in shallow water ranging in depth from 47.0 to 60.0 cm (Table 2). Larvae were monitored for a short period and water levels continued to rise following this spawn.

Table 2. *In-situ* data associated with clusters of Alligator Gar eggs spawned at West Fork Mill Creek during 2007, 2008, 2010, and 2013 in the Fourche LaFave River watershed. Means are reported with standard deviation in parentheses.

^a Some clusters of eggs were already exposed

^b Represents minimum distance from surface of water to egg

Alligator Gar yolk-sac larvae from the 17 June 2007 spawn event at WFMC hatched from 19 June (approximately 25 to 50% hatched relative to number of eggs present) to 20 June (approximately 90 - 100% hatched relative to number of eggs present). Incubation time was between 48 and 72 hours, with a sub-surface water temperature range of 27.5-30.0°C. On 19 June, over 1,000 yolk-sac larvae were observed attached (via the adhesive organ) and hanging vertically to live and dead herbaceous vegetation (e.g., *Carex* sp.) (Figure 4B) and woody debris (e.g., sticks and limbs) (Figure 4C). Multiple yolk-sac larvae were often observed hanging from the same object and when agitated, would detach and swim vigorously to the next available attachment site, including the surface tension of the water. Ten individuals were collected having a mean total length of 8.6 mm (SD, 0.6). On 20 June (3 days post spawn), over 1,000 yolk-sac larvae were again observed still attached and sedentary. Six additional yolk-sac larvae were collected and had a mean total length of 11.0 mm (SD, 1.3). Despite intensive visual searching on 24 June (7 days post spawn), no Alligator Gar larvae were found in WFMC; this corresponded with further flooding and probable change to exogenous feeding and a more active lifestyle.

Alligator Gar eggs were observed in four larger and more scattered clusters (30 - 200 cm diameter per cluster) on 15 June 2008 (Table 2). Eggs were found within 200 m upstream of the culverts which is a different location from other years. A majority of eggs were adhered to submerged limbs and leaves of woody shrubs and floating woody debris in shallow water. However, a few stray eggs were also found on live, inundated herbaceous vegetation, despite its limited presence (extended high water preceding the spawn season inhibited growth of herbaceous wetland vegetation). The day after spawn, nearly all eggs were found stranded above the surface of the water (submerged eggs were encased in fungus) because of lowering water levels. The June 2008 spawn occurred at an overall lower water level than during 2007, and little herbaceous vegetation was available. No larvae were found from this spawn.

On the afternoon of 23 May 2010, we searched much of the habitat upstream of the road crossing but only found egg clusters in the area where spawning was observed that morning. Five egg clusters were observed at water depths ranging from 70 to 90 cm (Table 2). Greatest density of eggs was attached to *Carex lupulina*, and eggs were within the top 20 cm of the vegetation. By \sim 1800 hours, eggs were already being exposed and desiccated. Water levels continued to lower, and at 1530 hours on 24 May 2010, 100% of the spawn location was dry and all eggs were desiccated (Figure 4D). No larvae were found from this spawn.

The spawn of 3 June 2013 probably resulted in more eggs, as indicated by number of clusters and cluster sizes, than observed in previous years (Table 2). Initial egg data were collected beginning at 1730 hours during the afternoon of 3 June. Ten clusters were identified at water depths ranging from 52.0 to 91.0 cm. Two of these clusters were expansive, extending up to 12.0 m in diameter; both clusters were in beds of *Carex lupulina*. Other clusters were in patches of *Carex lupulina* or *Carex triangularis* (Eastern Fox Sedge). Eggs adhered to the top portions of these plants, and were only up to \leq 14.0 cm from the surface. Egg clusters were marked with flagging, and monitored through 11 June 11 as water levels continued to decrease. Only 33% of egg clusters were viable on 5 June and measured eggs ranged in diameter (longest axis) from 4.2 to 5.3 mm; water temperature ranged from 25.1- 28.7°C and dissolved oxygen ranged from 2.7-4.2 mg/L. We found evidence of hatching on 5 June (two days post spawn), but fewer than ten yolk sac larvae were observed (7.1 to 7.9 mm TL) attached vertically to vegetation. On 6 June water temperature

was 25.7°C and dissolved oxygen was 2.61 mg/L. Forty-three yolk-sac larvae were observed across the flagged clusters, and approximately 98% of eggs that had not hatched were dead from desiccation and fungus. On 8 June (5 days post spawn) water temperature was 27.2° C and dissolved oxygen was 2.26 mg/L. Eighty-three yolk-sac larvae (11.2 to 12.9 mm TL) were observed at or in the vicinity of the flagged clusters. Most individuals had absorbed much of their yolk but were still vertically attached to vegetation and debris when found. These larvae were notably more mobile when disturbed. On 11 June (8 days post spawn) water temperature was 29.3C and dissolved oxygen was 3.27 mg/L. Seven larvae (13.5 to 18.3 mm TL) were found in the vicinity of the clusters. Larvae were all free-swimming, associated with cover, and oriented near the surface of the water.

DISCUSSION

We directly observed Alligator Gar spawning at the West Fork Mill Creek (WFMC) study site during four different years and have evidence of spawning in two additional years based on capture of Age-0 juveniles (unpublished data). Continued use of the same site for spawning indicates spawning site fidelity by this population of Alligator Gar, a phenomenon also observed in longnose gar (*Lepisosteus osseus*) in Missouri (Johnson and Noltie 1996) and suspected of Alligator Gar in southern Mississippi (R. Campbell, USFWS, personal communication). Whether the same adults or recruits successfully spawned at the site are returning to WFMC is unknown. The entire habitat area encompassing all spawning activity was only 0.10 km^2 , and even more remarkably, most spawn events across years spanned 300 m of the same ephemeral channel (Figure 2 and Figure 4D) often less than 100 m from each other. Evidence of Alligator Gar spawning was only found associated with floodplain tributary habitat. Consistent use across years of not only the same general area, but specific habitats for spawning indicates the value of the fine-scale habitat data collected during this study and the overall value of the WFMC site to furthering our understanding of Alligator Gar reproductive ecology. In contrast to the more specialist spawning requirements exhibited by Alligator Gar, *Lepisosteus* spp. YOY were distributed across all habitats surveyed, indicative of more generalist spawning requirements supported by other research and their large population sizes [e.g., Spotted Gar (Robison and Buchanan 2020)]. Our study highlights the importance of tributary habitat and access to herbaceous wetland vegetation to the perpetuation of the FLR/Arkansas River Alligator Gar population and overall significance of connected riverfloodplain habitat, particularly floodplain tributaries, within modified riverscapes.

General spawning behavior observed during our study was typical of gars (Suttkus 1963; Echelle and Grande 2014) and closely resembled observations of Longnose Gar spawning by Haase (1969) and captive Spotted Gar spawning by Frenette and Snow (2016) in terms of circular swimming paths by groups, a lead individual (presumably a female) followed by males, and thrashing of shallow water as gametes were emitted. Alligator Gar spawning group sizes in our study were similar to group sizes (four to 12 individuals) reported in Lake Texoma by Brinkman (2020) and St. Catherine Creek National Wildlife Refuge (up to 10 individuals) (K. Kimmel, USFWS, personal communication). Number of adults comprising spawning groups at WFMC during 2013 was notably higher than in previous years. Interestingly, the increase was due to a higher number of smaller fish that were likely from the 2007 spawn based on size at age data from Texas (Buckmeier et al. 2012). Sex ratios of gar spawning groups are generally expected to be male-skewed (Echelle and Grande 2014). We could not accurately estimate the sex ratio of the

spawning aggregation during 2013, but verified males tended to be smaller. Most spawning activity we documented was during early to midmorning hours (2007 being the exception), lasting 2-5.5 hrs. Overall, adults were in the spawning area for a relatively short time period (3.5-10 hrs., mean of 6.5 hrs.), perhaps an adaptation to minimize threat of predation and desiccation/stranding given the large size of adults in shallow water.

The mid May to mid June spawning season observed for Alligator Gar in the FLR generally corresponded with rising water levels (mostly due to backflooding from the Arkansas River) and increased water temperatures, which has been demonstrated to provide optimal environmental conditions for successful spawning and recruitment in riverine fishes (Junk et al. 1989; Turner et al. 1994; Johnson and Noltie 1996; Snedden et al. 1999; King et al. 2003). In several species increase in river flow and water level during the reproductive season is known to cue spawning in riverine fishes such as *Lepisosteus* spp., *Dorosoma* spp., catostomids, and *Pomoxis* spp. (Turner et al. 1994; Johnson and Noltie 1996; Killgore and Baker 1996; Snedden et al. 1999; Sammons et al. 2002; Adams et al. 2006). Data from the current study and other studies of Alligator Gar reviewed by Buckmeier et al. (2017) suggest the coupling between the ascending limb of a flood event (or increasing water levels) and a water temperature of 20°C or higher triggers spawning. When considering water temperature cues, it is important to consider temperature regimes in both the staging and spawning habitats and their spatial orientation (Allen et al. 2014). In our system temperatures were at least 20°C in both the staging habitat (mainstem FLR) and floodplain habitat (WFMC) to cue movement of adult Alligator Gar into spawning habitat and subsequent spawning. Floodplain temperatures we measured during spawning were usually warmer (2010 was the exception) than main channel FLR temperatures by 1.25°C to 1.8°C, a lower temperature differential than observed during spawning in the Lower Mississippi River (\sim 5 \degree C; Allen et al. 2020). In contrast to some systems where flooding cues are caused by increased discharge directly within the watershed due to local rainfall (e.g., Johnson and Noltie 1996), Alligator Gar in the FLR spawned during flood events caused primarily by back flow from the Arkansas River, not from elevated discharge from upstream within the FLR watershed. In terms of river network connectivity at large spatial scales, it is important to consider that spawning by Alligator Gar inhabiting the medium-sized FLR was highly dependent on elevated discharges and flooding of the larger Arkansas River. In an unregulated system, the evolved behavior of spawning as flooding commences or near flood peaks in response to major watershed events may be advantageous (*sensu* Junk et al. 1989). However, this reproductive strategy might be less advantageous in dam-regulated rivers that tend to have more extreme and erratic hydrological fluctuations with higher flood peaks and more rapid change (Sparks et al. 1998).

Gars in general, including Alligator Gar, evolved to spawn in structured environs typically having vegetation based on having adhesive, demersal eggs and larvae with adhesive organs on their snout (Echelle and Grande 2014). Alligator Gar reportedly spawn in association with flooded herbaceous and woody vegetation, including shrubs (reviewed by Buckmeier et al. 2017). Our observations are in general agreement with other reports, with the exception that herbaceous wetland vegetation, in particular *Carex lupulina*, was primarily used at our site, despite the presence of inundated leafy limbs of shrubs, small trees, and nearby cropland during all years. The only year we found eggs attached to shrubs was during 2008 when the spawn was interrupted by decreasing water levels and wetland vegetation was sparse. *Carex lupulina* is a native, perennial sedge commonly associated with wetlands throughout the southeastern United States (Schummer

et al. 2012), and this species is considered a wetland "obligate" by the U.S. Army Corps of Engineers National Wetland Plant List (https://wetland-plants.sec.usace.army.mil/nwpl). *Carex lupulina* tends to form dense clumps or beds at our study site. During most years, it was abundantly available within and bordering the ephemeral ditch that gar typically spawned in association with (Figure 4D). The pliant leaf blades of this large sedge species kept their vertical form during initial inundation, providing a dense vertical substrate near the surface for egg dispersal (versus on the bottom) and providing attachment refugia for larvae (Figure 4B). The leaf blades mostly lay over, presumably due to the weight of egg masses and trashing of spawning gar, and naturally remain on the surface at or below the interface as water levels lowered, a potential benefit of eggs adhering to a flexible substrate versus a rigid, sturdy substrate as we observed during 2008 (e.g., shrubs). Shallow, vegetated habitats provide protection from predators and accelerated development of eggs and larvae due to elevated temperatures (Ward and Stanford 1995). Most sedges and many other common herbaceous wetland plants are associated with open environments not shaded by woody vegetation and not disturbed by agricultural practices (Schummer et al. 2012). These factors should be considered when conserving this important aspect of the floodplain mosaic for Alligator Gar spawning and rearing habitat. In addition, spawning habitat suitability models that weight inundated herbaceous wetland vegetation equally with other types of herbaceous habitats (e.g., cropland, pasture/grassland, and shrubs) could be overestimating optimal spawning habitat availability as cropland and pasture were readily available in the lower FLR and in close proximity to our primary spawning area (Figure 2). More detailed field observations of specific spawning substrates used relative to availability are needed from additional sites and rivers to understand how specific or general Alligator Gar utilize types of vegetation, but most existing observations have occurred in herbaceous wetland vegetation (Buckmeier et al. 2017).

Floodplain tributaries functioned as both movement corridors and spawning and nursery habitat for Alligator Gar in the FLR riverscape. Other accounts of spawning habitat are from adjacent floodplain areas such as oxbow lakes (Cook 1959; Robertson et al. 2008), connected backwater complexes and floodplain lakes (R. Campbell and K. Kimmel, USFWS, personal communication) (Allen et al. 2014), or shallow littoral areas adjacent to a reservoir (May and Echelle 1968; Garcia de León et al. 2001; Brinkman 2020) or river (Pigg and Gibbs 1996). Although oxbow lakes, floodplain ponds, and other shallow, flooded areas were available for spawning and rearing, evidence of reproduction in the FLR was limited to lowland tributaries and associated habitats. A primary factor is degree of connectivity between adult staging areas in the FLR channel and access to low elevation, herbaceous vegetation on the ascending flood limb. Oxbow lakes and floodplain ponds of the FLR tend to be perched on the floodplain, disconnected from the main channel except during large magnitude floods, and lack connecting channels (Naus and Adams 2018). In contrast, floodplain tributaries, such as WFMC, are connected with the main channel at base flow and provide reliable access to herbaceous vegetation further on the floodplain as flooding begins, thus utilizable by large-bodied adults over a wider range of flood elevations. Maintaining passage within travel corridors connecting adult staging and spawning/rearing habitats is important to consider from a conservation perspective, and corridor characteristics should be considered when examining suitable Alligator Gar spawning habitats at large spatial scales.

Alligator Gar have an overall life history strategy making them vulnerable to anthropogenic disturbances (Winemiller and Rose 1992), and our research has identified other aspects of concern specific to spawning and early life stages that should be a focus of conservation of river-floodplain populations. Access to shallow, structured floodplain habitats are essential for spawning success. Spawning and rearing locations should be identified in rivers and potential barriers to movement between river channels and floodplain spawning areas should be addressed. For example, to reach the WFMC spawning area, adults passed a county road by swimming through culverts or over the road, depending on water levels, a common challenge for riverine fishes trying to access the floodplain. Failing culverts were replaced during fall 2010 with improved structures intended to facilitate more reliable fish passage. Alligator Gar laid eggs in shallow water, often only 14 cm or less from the surface, and early larval stages were mostly sedentary, needing ~ 8 days post spawn to reach a more active developmental stage. Rate of development will vary with water temperature, and most of our field observations of eggs and larvae were near the optimal hatching and development water temperature of 27.7°C reported by Long et al. (2020). Additionally, our larval growth rates observed in 2007 (\sim 3.6 mm TL/day) and 2013 (\sim 4.0-5.0 mm TL/day), based on comparing our time series of larval lengths, were very similar to growth rates reported by Sakaris et al. (2019). Early life stages are highly vulnerable to lowering water levels, and we observed desiccation during multiple years following spawning. Rivers within the range of Alligator Gar tend to have a modified (usually more variable) hydrology, and biologists should search for opportunities to extend the inundation period of spawning areas following floods during the spawning season when practical and necessary (*sensu* Poff et al. 1997; Snow and Long 2015). Lastly, large-bodied adults in very shallow water are highly vulnerable to bowfishing, and were targeted by bowfishers at our study site. Environmental conditions conducive to reproductive success do not occur every year, and Alligator Gar should be protected while spawning. For example, the Arkansas Game and Fish Commission passed a regulation in 2010 prohibiting recreational take of Alligator Gar during the spawning season, setting an example for some other natural resource agencies within the range of Alligator Gar (Smith et al. 2020).

Floodplain Habitat Management

Prior to settlement, the historic wetland and prairie floodplains of the Mississippi River and its large tributaries were a heterogeneous, successional mosaic maintained by both stochastic and consistent disturbances from floods, scour, fire (wild and native set), and animal influenced (Fisk 1945; Grossman et al. 1982; Nelson et al. 1998; Naiman et al. 2000; Ward et al. 2001; Robinson et al. 2002; Jacobson et al. 2011). By recent assessments, the Lower Mississippi River Valley has lost over 1.4 million hectares of direct floodplain and ~8.5 to 10.1 million hectares of wetlands (85-90%) to levees (Baker et al. 1991; Sparks et al. 1998; Haynes 2004). Much of the connected floodplain that remains consists of homogenous riparian forests or cropland (USGS, National Land Cover Database 2016), neither of which has been directly observed to provide spawning habitat for Alligator Gar nor are they typical spawning habitats of other native large river fishes that attach eggs to herbaceous vegetation [e.g., other gars and buffaloes (Echelle and Grand 2014; Robison and Buchanan 2020)]. Further, only \sim 5% of floodplain area within the Lower Mississippi River is comprised of natural, early successional vegetation (Allen et al. 2020). In the lower FLR, only \leq 2.1% LULC may have provided suitable habitat for spawning and rearing of egg and larval stages (1.1% emergent herbaceous wetland; 1.0% grassland/herbaceous; < 1.0% shrub/scrub). The estimated 30-70% decline (Nature Serve) in historic range of Alligator Gar and habitat may be far greater considering the extensive loss of historical habitat heterogeneity, including early successional herbaceous spawning habitat as described in this study; altered hydrology; reduction in natural landscape successional resetting disturbances; and lateral disruptions to connectivity

(Sparks 1995; Sparks et al. 1998). We must consider all of the available historical accounts of the landscape and range of the species, along with recently obtained knowledge, to fully comprehend change and realize pragmatic conservation for Alligator Gar (Pauly 1995; Ward et al. 2001; Keevin and Lopinot 2019). Comprehensive and substantive rehabilitation objectives may be achieved through adaptive management and modified conservation programs, smaller-scale barrier removals, structure modifications, management plan alterations, reintroductions, hydroperiod manipulations, controlled burns, revised beaver management, reintroduction of natural or humaninduced disturbance regimes, and integrated conservation practices applied consistently to link these river corridor habitats and recreate a managed, shifting habitat mosaic across the landscape (Sparks et al. 1998; Ward et al. 2002; Stanford et al. 2005; Nel et al. 2009).

Many floodplain conservation management plans, programs, and practices have been developed for wetland and ecosystem restoration but often with only cursory or non-specific integration of fish conservation and restoration objectives (Leao 2005; King et al. 2006). Their common goal is to restore the greatest wetland functions, values, and services through construction of a heterogeneous landscape with a hydroperiod that will maintain a variety of wetland habitats and diversity of species, with some targeted focal species; however, they often only provide broadscale consideration to fish, placing primary focus on bottomland hardwoods, waterfowl, and/or biodiversity with little or no habitat heterogeneity on the site or at the landscape level (Ward et al. 2001; Faulkner et al. 2011). Many uniquely-adapted fishes complete their life cycles in forested wetlands in the southern United States or utilize this habitat facultatively (Killgore and Baker 1996; Hoover an Killgore 1998). However, as an obligate spawner in open canopied, early successional floodplain habitats, Alligator Gar should be a focal species to ensure conservation programs, such as the Wetland Reserve Program (WRP), Conservation Reserve Program (CRP), and other federal compensatory mitigation programs (along with federal and state conservation agencies' management areas plans), include floodplain fish conservation, habitat heterogeneity, and availability of herbaceous wetland vegetation in their conservation objectives and goals rather than a primary focus on reforestation.

LITERATURE CITED

- Adams, S. R., M. B. Flinn, B. M. Burr, M. R. Whiles, and J. E. Garvey. 2006. Ecology of larval blue sucker *(Cycleptus elongatus)* in the Mississippi River. Ecology of Freshwater Fish 15: 291-300.
- Aguilera, C., R. Mendoza, G. Rodriguez, and G. Marquez. 2002. Morphological description of Alligator Gar and tropical gar larvae, with an emphasis on growth indicators. Transactions of the American Fisheries Society 131: 899-909.
- Allen, Y.C, K. M. Kimmel, and G. C. Constant. 2014. Alligator Gar movement and water quality patterns on the St. Catherine Creek National Wildlife Refuge floodplain. U.S. Fish and Wildlife Service. Baton Rouge Fish and Wildlife Conservation Office report.
- Allen, Y., K. Kimmel, and G. Constant. 2020. Using remote sensing to assess Alligator Gar spawning habitat suitability in the lower Mississippi River. North American Journal of Fisheries Management 40: 580-594.
- Baker, J. A., K. J. Killgore, and R. T. Kasul. 1991. Aquatic habitats and fish communities in the lower Mississippi River. Reviews in Aquatic Sciences 3: 313-356.
- Brinkman, E. L., and W. L. Fisher. 2020. Life history characteristics of Alligator Gar (*Atractosteus spatula*) in the upper Red River (Oklahoma–Texas). The Southwestern Naturalist 64: 98- 108.
- Buckmeier, D. L., N. G. Smith, and K. S. Reeves. 2012. Utility of Alligator Gar age estimates from otoliths, pectoral fin rays, and scales. Transactions of the American Fisheries Society 141: 1510-1519.
- Buckmeier, D. L., N. G. Smith, D. J. Daugherty, and D. L. Bennett. 2017. Reproductive ecology of Alligator Gar: identification of environmental drivers of recruitment success. Journal of the Southeastern Association of Fish and Wildlife Agencies 4: 8-17.
- Burr, J. G. 1931. Electricity as a means of garfish and carp control. Transactions of the American Fisheries Society 61: 174-182.
- Cook, F. A. 1959. *Freshwater fishes in Mississippi*. Mississippi Game and Fish Commission, Jackson, Mississippi.
- Etnier, D. A., and W. C. Starnes. 1993. *The fishes of Tennessee*. University of Tennessee Press, Knoxville, Tennessee.
- Echelle, A., and L. Grande. 2014. Lepisosteidae: gars. Pages 243-278. *in* M. L. Warren, Jr. and B. M. Burr editors. *Freshwater fishes of North America Volume 1: Petromyzontidae to Catostomidae*. Johns Hopkins University Press, Baltimore.
- Echelle, A. A., and C. D. Riggs. 1972. Aspects of the early life history of gars (*Lepisosteus*) in Lake Texoma. Transactions of the American Fisheries Society 101: 106-112.
- Faulkner, S., W. Barrow, B. Keeland, S. Walls, and D. Telesco. 2011. Effects of conservation practices on wetland ecosystem services in the Mississippi Alluvial Valley. Ecological Applications, Special Publication 21: 31-48.
- Ferrara, A. M. 2001. Life-history strategy of Lepisosteidae: implications for the conservation and management of Alligator Gar. Ph.D. Dissertation, Auburn University, Alabama.
- Fisk, H. N. 1945. Geological investigation of the alluvial valley of the lower Mississippi River. U.S. Department of the Army, Mississippi River Commission.
- Frenette, B. D., and R. Snow. 2016. Natural habitat conditions in a captive environment lead to spawning of Spotted Gar. Transactions of the American Fisheries Society 145: 835-838.
- Garcia de León, F. J., L. González-García, J. M. Herrera-Castillo, K. O. Winemiller, and A. Banda-Valdés. 2001. Ecology of the Alligator Gar, *Atractosteus spatula*, in the Vicente Guerrero Reservoir, Tamaulipas, Mexico. The Southwestern Naturalist 46: 151-157.
- Grossman, G. D., P. B. Moyle, and J. P. Whitaker. 1982. Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: a test of community theory. The American Naturalist 120: 423-454.
- González, C. A., J. A. Cruz, and R. M. Alfaro. 2015. Physiological response of Alligator Gar juveniles (*Atractosteus spatula*) exposed to sub-lethal doses of pollutants. Fish Physiology and Biochemistry 41: 1015-1027.
- Haase, B. L. 1969. An ecological life history of the Longnose Gar, *Lepisosteus osseus* (Linnaeus), in Lake Mendota and in several other lakes of southern Wisconsin. Ph.D. Dissertation, University of Wisconsin, Madison.
- Haynes, R. J. 2004. The development of bottomland forest restoration in the Lower Mississippi River Alluvial Valley. Ecological Restoration 22: 170-182.
- Hoover, J. J., and K. J. Killgore. 1998. Fish Communities. Pages 237-260. *in* M. G. Messina and W. H. Conner editors. *Southern Forested Wetlands: Ecology and Management*, CRC Press.
- Inebnit III, T. E. 2009. Aspects of the reproductive and juvenile ecology of Alligator Gar in the Fourche LaFave River, Arkansas. M.S. Thesis, University of Central Arkansas, Conway, Arkansas.
- Jacobson, R. B., T. P. Janke, and J. J. Skold. 2011. Hydrologic and geomorphic considerations in restoration of river-floodplain connectivity in a highly altered river system, Lower Missouri River, USA. Wetlands Ecology and Management 19: 295-316.
- Jelks, H. L., S. J. Walsh, N. M. Burkhead, S. Contreras-Balderas, E. Diaz-Pardo, D. A. Hendrickson, J. Lyons, N. E. Mandrak, F. McCormick, J. S. Nelson, S. P. Platania, B. A. Porter, C. B. Renaud, J. J. Schmitter-Soto, E. B. Taylor, and M. L. Warren Jr. 2008. Conservation status of imperiled North American freshwater and diadromous fishes. Fisheries 33: 372-407.
- Johnson, B. L., and D. B. Noltie. 1996. Migratory dynamics of stream-spawning longnose gar (*Lepisosteus osseus*)*.* Ecology of Freshwater Fish 5: 97-107.
- Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The flood pulse concept in river floodplain systems. Pages 110-127. *in* D. P. Dodge, editor. Proceedings of the International Large River Symposium. Canadian Special Publication of Fisheries and Aquatic Sciences.
- Keevin T. M., and N. H. Lopinot. 2019. Historical record of an Alligator Gar, *Atractosteus spatula*, captured on the floodplain of the Middle Mississippi River at Columbia, Illinois, USA. Journal of Applied Ichthyology 35: 871–875.
- King, A. J., P. Humphries, and P. S. Lake. 2003. Fish recruitment on floodplains: the roles of patterns of flooding and life history characteristics. Canadian Journal of Fisheries and Aquatic Sciences 60: 773-786.
- King, S. L., D. J. Twedt, and R. R. Wilson. 2006. The role of the Wetland Reserve Program in conservation efforts in the Mississippi River Alluvial Valley. Wildlife Society Bulletin 34: 914-920.
- Killgore, K. J., and J. A. Baker. 1996. Patterns of larval fish abundance in a bottomland hardwood wetland. Wetlands 16: 288-295.
- Kluender, E. R., R. Adams, and L. Lewis. 2017. Seasonal habitat use of Alligator Gar in a river– floodplain ecosystem at multiple spatial scales. Ecology of Freshwater Fish 26: 233-246.
- Leao, M. 2005. Fish utilization and diversity associated with created wetlands within the lower White River watershed, Arkansas. Ph.D. Dissertation. University of Arkansas at Pine Bluff, Pine Bluff, Arkansas.
- Lochmann, S., E. L. Brinkman, and D. A. Hann. 2021. Movements and macrohabitat use of Alligator Gar in relation to a low head lock and dam system. North American Journal of Fisheries Management 41: 204-216.
- Long, J. M., R. A. Snow, and M. J. Porta. 2020. Effects of temperature on hatching rate and early development of Alligator Gar and Spotted Gar in a laboratory setting. North American Journal of Fisheries Management 40: 661-668.
- May, E. B., and A. A. Echelle. 1968. Young of year Alligator Gar in Lake Texoma, Oklahoma. Copeia 1968: 629-630.
- Mendoza, R., C. Aguilera, G. Rodriquez, M. Gonzalez, and R. Castro. 2002. Morphophysiological studies on Alligator Gar (*Atractosteus spatula*) larval development as a basis for their culture and repopulation of their natural habitats. Reviews in Fish Biology and Fisheries 12: 133- 142.
- Mendoza-Alfaro, R., C. Aguilera Gonzalez, and A. M. Ferrara. 2008. Gar biology and culture: status and prospects. Aquaculture Research 39: 748 – 763.
- Moore, G. A., M. B. Trautman, and M. R. Curd. 1973. A description of post larval gar (*Lepisosteus spatula,* Lacepede, Lepisosteidae), with a list of associated species from the Red River, Choctaw County, Oklahoma. The Southwestern Naturalist 18: 343-344.
- Naiman, R. J., R. E. Bilby, and P. A. Bisson. 2000. Riparian ecology and management in the Pacific coastal rain forest. BioScience 50: 996-1011.
- Naus, C. J., and S. R Adams. 2018. Fish nursery habitat function of the main channel, floodplain tributaries and oxbow lakes of a medium‐sized river. Ecology of Freshwater Fish 27: 4-18.
- Nel, J. L., D. J. Roux, R. Abell, P. J Ashton, R. M. Cowling, J. V. Higgins, M. Thieme, and J. H. Viers. 2009. Progress and challenges in freshwater conservation planning. Aquatic Conservation: Marine and Freshwater Ecosystems 19: 474-485.
- Nelson, J. C., R. E. Sparks, L. DeHaan, and L. Robinson. 1998. Presettlement and contemporary vegetation patterns along two navigation reaches of the Upper Mississippi River. Perspectives on the land-use history of North America: a context for understanding our changing environment. U.S. Geological Survey, Biological Resources Division USGS/BRD/BSR-1998-0003:51-60.
- O'Connell, M. T., T. D. Shepherd, A. M. U. O'Connell, and R. A. Myers. 2007. Long-term declines in two apex predators, Bull Sharks (*Carcharhinus leucas*) and Alligator Gar (*Atractosteus spatula*), in Lake Pontchartrain, an oligohaline estuary in southeastern Louisiana. Estuaries and Coasts 30: 567 – 574.
- Pauly, D. 1995. Anecdotes and the shifting baselines syndrome of fisheries. Trends in Ecology & Evolution 10: 430.
- Pigg, J., and R. Gibbs. 1996. Observations on the propagation of two rare fish species in Oklahoma. Proceedings of the Oklahoma Academy of Science 76: 89.
- Poff N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime: a paradigm for river conservation and restoration. BioScience 47: 769–784.
- Robertson, C. R., K. Aziz, D. L. Buckmeier, N. G. Smith, and N. Raphelt. 2018. Development of a flow‐specific floodplain inundation model to assess Alligator Gar recruitment success. Transactions of the American Fisheries Society 147: 674-686.
- Robertson, C. R., S. C. Zeug, and K. O. Winemiller. 2008. Associations between hydrological connectivity and resource partitioning among sympatric gar species (Lepisosteidae) in a Texas river and associated oxbows. Ecology of Freshwater Fish 17: 119-129.
- Robinson, C. T., K. Tockner, and J. V. Ward. 2002. The fauna of dynamic riverine landscapes. Freshwater Biology 47: 661-677.
- Robison, H. W., and T. M. Buchanan. 2020. Fishes of Arkansas. 2nd edition. The University of Arkansas Press, Fayetteville, Arkansas.
- Sakaris, P. C., D. L. Buckmeier, N. G. Smith, and D. J. Daugherty. 2019. Daily age estimation reveals rapid growth of age-0 alligator gar in the wild. Journal of Applied Ichthyology 35: 1218-1224.
- Sammons, S. M., P. W. Bettoli, D. A. Isermann, and T. N. Churchill. 2002. Recruitment variation of crappies in response to hydrology of Tennessee reservoirs. North American Journal of Fisheries Management 22: 1393-1398.
- Scarnecchia, D. L. 1992. A reappraisal of gars and bowfins in fishery management. Fisheries 17: 6-12.
- Schummer, M. L., H. M. Hagy, K. S. Fleming, J. C. Cheshier, and J. T. Callicutt. 2012. *A guide to moist-soil wetland plants of the Mississippi Alluvial Valley*. University Press of Mississippi, Jackson, Mississippi.
- Smith, N. G., D. J. Daugherty, E. L. Brinkman, M. G. Wegener, B. R. Kreiser, A. M. Ferrara, K. D. Kimmel, and S. R. David. 2020. Advances in conservation and management of the Alligator Gar: a synthesis of current knowledge and introduction to a special section. North American Journal of Fisheries Management 40: 527-543.
- Snedden, G. A., W. E. Kelso, and D. A. Rutherford. 1999. Diel and seasonal patterns of Spotted Gar movement and habitat use in the lower Atchafalaya River Basin, Louisiana. Transactions of the American Fisheries Society 128: 144-154.
- Snow, R. A., and J. M. Long. 2015. Estimating spawning times of Alligator Gar (*Atractosteus spatula*) in Lake Texoma, Oklahoma. Proceedings of the Oklahoma Academy of Science 95: 46-53.
- Sparks, R. E. 1995. Need for ecosystem management of large rivers and their floodplains. BioScience 45: 168-182.
- Sparks, R.E., J. C. Nelson, and Y. Yin. 1998. Naturalization of the flood regime in regulated rivers: the case of the upper Mississippi River. BioScience 48: 706-720.
- Stanford, J. A., M. S. Lorang, and F. R. Hauer. 2005. The shifting habitat mosaic of river ecosystems. Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen 29: 123-136.
- Suttkus, R. D. 1963. Order Lepisostei. Pages 61-88. *in* Bigelow, H. B., and W. C. Schroeder, editors. *Fishes of the western North Atlantic*. Memoirs of the Sears Foundation for Marine Research I, part 3. New Haven, Connecticut.
- Turner, T. F., J. C. Trexler, G. L. Miller, and K. E. Toyer. 1994. Temporal and spatial dynamics of larval and juvenile fish abundance in a temperate floodplain river. Copeia 1994:174-183.
- van der Most, M., and P. F. Hudson. 2018. The influence of floodplain geomorphology and hydrologic connectivity on Alligator Gar (*Atractosteus spatula*) habitat along the embanked floodplain of the Lower Mississippi River. Geomorphology 302: 62-75.
- Wallus, R., T. P. Simon, and B. L. Yeager. 1990. *Reproductive biology and early life history of fishes in the Ohio River Drainage: Acipenseridae through Esocidae*. Tennessee Valley Authority, Chattanooga, Tennessee.
- Ward, J V., and J. A. Stanford. 1995. Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. Regulated Rivers: Research and Management 11: 105-119.
- Ward, J. V., K. Tockner, U. Uehlinger, and F. Malard. 2001. Understanding natural patterns and processes in river corridors as the basis for effective river restoration. Regulated Rivers: Research and Management 17: 311-323.
- Ward, J. V., K. Tockner, D. B. Arscott, and C. Claret. 2002. Riverine landscape diversity. Freshwater Biology 47: 517-539.
- Winemiller, K.O., and K. A. Rose. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. Canadian Journal of Fisheries and Aquatic Sciences 49: 2196-2218.