*Transactions of the American Fisheries Society*, 2025, **154**, 115–126
https://doi.org/10.1093/tafafs/vnae006
Advance access publication: March 27, 2025
**Article**

# Spotting gar using imaging sonar: The effects of river–floodplain habitat connectivity on a lepisosteid assemblage

Adam H. Quade[1,2]*, Allyse Ferrara[3], Quenton Fontenot[3], Kelly S. Boyle[2], Solomon R. David[4], and Guillaume Rieucau[1]

[1]Louisiana Universities Marine Consortium, Chauvin, Louisiana, USA
[2]Department of Biological Sciences, University of New Orleans, New Orleans, Louisiana, USA
[3]Department of Biological Sciences, Nicholls State University, Thibodaux, Louisiana, USA
[4]Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul, Minnesota, USA

*Corresponding author: Adam H. Quade. Email: aquade@lumcon.edu.



## ABSTRACT

**Objective:** Anthropogenic modifications, such as levee construction and other flood control structures, have decoupled Louisiana's floodplains from the seasonal flood pulse, influencing aquatic food web dynamics. Many of Louisiana's fish species rely on timing, magnitude, and duration of the Mississippi River flood pulse to trigger key aspects of their life histories. At the Richard K. Yancey Wildlife Management Area, 283 ha of Mississippi River floodplain are undergoing weir and culvert repair to retain water depth and improve water quality for native Louisiana fishes, with particular focus on large nongame species, such as gars (Lepisosteidae).

**Methods:** Beginning in summer 2021, we conducted high-resolution imaging sonar monitoring of gar abundance, size-class distribution, and habitat use across seasons at four sites through a latitudinal gradient of decreasing hydrologic connectivity. We tested the hypothesis that the degree of river–floodplain connectivity, mediated by seasonal inundation levels and proximity to the Mississippi River, affects the abundance and size-class distribution of gar in the floodplain.

**Results:** Our study demonstrated size-class-dependent use of floodplain habitats that was mediated by inundation level but not by the distance from the Mississippi River. Our results suggest that remaining pools of water, when disconnected from the main-stem river, are likely to provide both nursery and refuge habitats to floodplain-associated gar.

**Conclusions:** Continued monitoring efforts will provide additional data to better describe the complex interactions between floodplain-associated fishes and habitat use in relation to inundation level and hydrologic restoration efforts.

**KEYWORDS:** flood pulse, floodplain, gar, imaging sonar, Mississippi River

## LAY SUMMARY

Using high-resolution imaging sonar, we found that the use of floodplain habitats by the gar assemblage depends on the degree of Mississippi River–floodplain connectivity. This connectivity influences gar abundance and size distribution, with smaller gar likely relying on low-water habitats as nurseries and refuges.

## INTRODUCTION

Large river–floodplain systems are comprised of a mosaic of interconnected lowland habitats that experience different levels of inundation from the lateral overflow of the main-stem river driven by a seasonal flood pulse (Junk et al., 1989). An unconstrained flood pulse hydrologically links floodplain habitats and triggers abiotic and biotic interactions (Bayley, 1995; Junk et al., 1989; Sendek et al., 2021). Once connected, resources from aquatic and terrestrial zones mix, supporting high levels of productivity (Mosepele et al., 2022; Ochs & Shields, 2019; Oliveira et al., 2023). This connectivity further influences water quality; fish species abundance, diversity, and distribution; and trophic interactions (Baustian et al., 2019; Burdis et al., 2020; Jenney et al., 2022; Lindholm et al., 2007; McCoy et al., 2020; Mitsch et al., 2008).

Outside of the seasonal flood pulse, a floodplain maintains ecological importance for aquatic and terrestrial fauna even at low water levels (Bănăduc et al., 2021; Naus & Adam, 2018).

**Received:** June 25, 2024. **Revised:** November 7, 2024. **Editorial decision:** November 22, 2024

Receding floodwaters create isolated water bodies that may become disconnected from other water bodies on the floodplain and from the main-stem channel. Within these isolated water bodies, phytoplankton production is supported through increasing nutrient concentrations (Junk et al., 1989; Thomaz et al., 2007), which in turn helps to sustain upper trophic levels (Bayley, 1995). Aquatic fauna, such as fish, may use the remaining water bodies to persist between periods of floodplain inundation (Magoulick & Kobza, 2003). Assemblage composition (Arthington et al., 2005; Lorenzon et al., 2020) and size-class-specific habitat preferences (Richard et al., 2018) have also been documented, emphasizing the nuanced interactions between ecological communities and floodplain hydrology.

Large river–floodplain ecosystems, such as the lower Mississippi River basin (LMRB), are ecologically and economically important but have been heavily altered by anthropogenic modifications to control flooding (Eggleton et al., 2016). These modifications have drastically reduced the size of the historic LMRB floodplain from 10.1 million ha to less than 8% of its original size (Schramm & Ickes, 2016). In Louisiana, the construction of levees and other water control structures along much of the Mississippi River has disconnected floodplain habitats from the main-stem river and changed seasonal hydrology so that floodplain inundation only occurs during high precipitation events (Nelson et al., 2002). The irregular inundation of disconnected floodplains may have negative impacts on organisms with life histories adapted to high water in the spring and low water in the fall (Alford & Walker, 2013; King et al., 2009; Lytle & Poff, 2004), the typical hydrology of the Mississippi River (Eggleton et al., 2016; Kemp et al., 2014; Luo & Criss, 2018).

Gar species in the LMRB, which include Alligator Gar *Atractosteus spatula*, Spotted Gar *Lepisosteus oculatus*, Longnose Gar *L. osseus*, and Shortnose Gar *L. platostomus*, may use the flood pulse as an environmental life history cue. Gar in the southern United States typically leave the main-stem channel and low-water refuges to access the newly inundated floodplain when rising water level and increased temperature coincide in the spring (Bonvillain et al., 2008; Buckmeier et al., 2017; Roberts et al., 2023; Robertson et al., 2008; Smith, Buckmeire, et al., 2020; Smith, Daugherty, et al., 2020; Snedden et al., 1999; Wegener et al., 2017). Rising floodwaters that inundate terrestrial zones allow gar to exploit enhanced foraging opportunities and access spawning habitat (Buckmeier et al., 2013; Butler et al., 2018; McAllister et al., 2023; Robertson et al., 2008; Smylie et al., 2015). These species are negatively affected by anthropogenic activities in the Mississippi River floodplain, such as construction of levees and other water control structures that are designed to restrict floodwaters (Allen et al., 2020; David et al., 2018). Unsubstantiated claims of negative impacts on game fishes relegated gar into the "rough fish" category, and management techniques were implemented in the early to mid-1900s to actively reduce or eliminate gar populations (Scarnecchia, 1992). These misconceptions, coupled with the drastic reduction in the size of the LMRB floodplain, led to the extirpation of Alligator Gar from much of their native range, while other gar species remain relatively stable (Kluender et al., 2016; Scarnecchia, 1992; Smith, Buckmeire, et al., 2020). Perception has shifted as new research reveals the ecological (Butler et al., 2018; Smylie et al., 2015) and biomedical (Braasch et al., 2016) importance of Lepisosteidae and as anglers seek opportunities to catch large individuals (Bennett et al., 2015; Buckmeier et al., 2016; Schlechte & Buckmeier, 2021).

To date, the study of gar ecology and habitat use has been conducted using techniques that have implicit biases. Traditional techniques, such as electrofishing and gill nets, are often restricted to certain sizes of individuals or cannot operate effectively at various water depths (Buckmeier & Schlechte, 2009; Millar & Fryer, 1999; Ruetz et al., 2007). As such, multiple gear types and repeated efforts must be employed to capture a holistic understanding of the system, thus increasing the amount of induced disturbance (Pritt & Frimpong, 2014). Prior studies on gar and other species suggest that ascertaining fine-scale patterns (i.e., to the level of the individual) may remain challenging, as disturbances caused by traditional sampling gears may alter typical behaviors through the capture or removal of an individual (Benevides et al., 2019; Gilbert et al., 2001; Richardson & Flinn, 2019). Continued development of minimally invasive methods may have fewer biases compared to traditional techniques and may preserve the natural behaviors of both the assemblages and individuals.

Innovations in observational sampling technologies, such as imaging sonars, offer a means to study aquatic ecosystems down to the level of the individual through video-like data recorded in situ. Operating at high frequencies (0.7–3.0 MHz) beyond the hearing threshold of most aquatic fauna (Narins et al., 2013; Velez, 2015), imaging sonars may be used to obtain quantitative ecological and behavioral information without the biases of traditional techniques and are not limited by environmental factors like turbidity (Lyon et al., 2014; Speas et al., 2004). Recent research has established the ability of this technology to nonintrusively monitor complex habitats and resolve behavioral research gaps in highly turbid environments (for recent reviews, see Munnelly et al., 2023; Sibley et al., 2023; and Wei et al., 2022). Despite the now well-demonstrated performance of imaging sonars for studying behavioral interactions and associations with complex habitats and low-visibility environments, taxonomic resolution and species identification remain challenging (Munnelly et al., 2023). Identification using morphological characteristics becomes progressively easier with increasing body size (0.50 m and greater) and knowledge of body shape and swimming styles that can be viewed in video-like data sets.

Here, we used advanced high-resolution imaging sonar (Adaptive Resolution Imaging Sonar [ARIS] Explorer 3000; Sound Metrics Corporation, Bellevue, Washington) to quantify abundance and size-class distributions of native Louisiana gar species in a floodplain of the lower Mississippi River (Richard K. Yancey Wildlife Management Area [WMA]). In contrast to traditional sonars, which provide standard echolocation data, or side-scan and forward-facing sonars, which produce lower resolution images, ARIS imaging sonars use a greater number of beams and can operate at frequencies exceeding 1.8 MHz, resulting in a higher quality video-like data set. Gar, in general, are readily identifiable in ARIS footage from an elongated, fast-start predator body type and pronounced caudal fin swimming style. Our objective was to test the hypothesis that the degree of river–floodplain connectivity influences the abundance and size-class distribution of the gar assemblage while considering

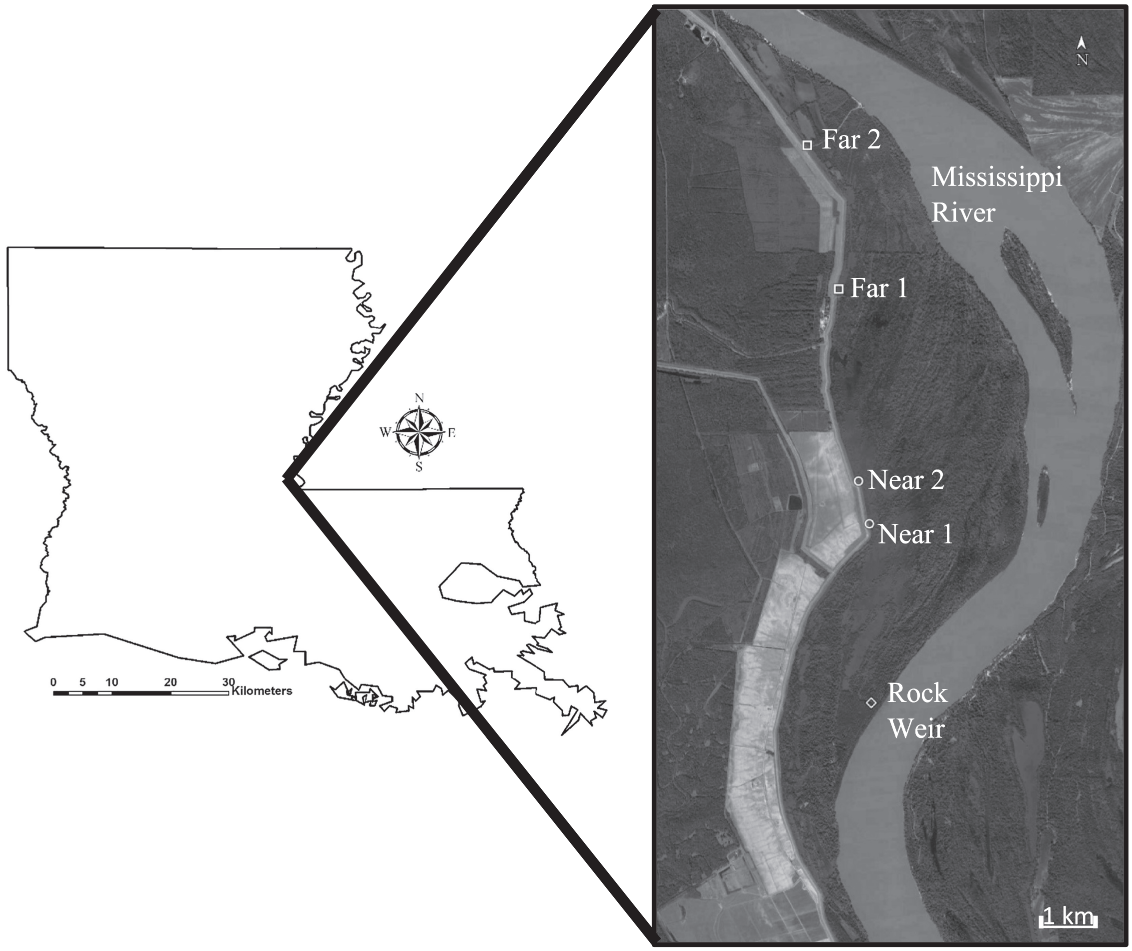


**Figure 1.** Map of Louisiana, with study sites in the Richard K. Yancey Wildlife Management Area depicted (inset). Circles represent sites that were relatively close to the point of Mississippi River inundation (near sites); squares represent sites that were relatively far from the inundation point (far sites). The diamond represents the rock weir, which is the initial inundation point for the management area.

seasonal variation. To achieve this, we conducted imaging sonar surveys targeting periods of high water (connected) and low water (disconnected) across all four seasons (spring, summer, fall, and winter) at four fixed sites that retain water during low-water periods and are located at different distances from the point where Mississippi River water flows onto the floodplain. This study was conducted prior to planned hydrologic restoration efforts at the Richard K. Yancey WMA, providing a critical baseline for future comparisons of gar abundance and size-class distribution in response to these efforts.

## METHODS

### Study site

The study was conducted at the Richard K. Yancey WMA (Louisiana Department of Wildlife and Fisheries) near Vidalia, Louisiana, between August 7, 2021, and January 20, 2023. The WMA (31.18896, −91.63190) comprises approximately 28,328 ha of floodplain habitat located on the western bank of the Mississippi River floodplain. The terrain is typically flat, with flora consisting of mixed bottomland hardwoods. Three lakes in the southern areas of the WMA remain inundated year-round but are disconnected from the Mississippi River during low-water periods and are the first habitats to become connected to the main stem by the seasonal flood pulse. As floodwaters rise, the lakes connect to the northern portion of the floodplain through a series of culverts and bayous. Our study focused on the 283 ha of the WMA designated for future hydrologic restoration via culvert (31.12166, −91.62435; and 31.21497, −91.63407) and weir (31.145117, −91.626094) repair/replacement to improve water quality and facilitate fish passage (Figure 1). At the time of the study, the WMA still contained a rock weir that was slated for repair. Located in the southern bounds of the floodplain lake nearest to the Mississippi River, the rock weir (along with the eventual replacement) serves as the initial point of inundation in the WMA, as natural geographic features and historic anthropogenic modifications (e.g., levees) prevent floodwaters from entering elsewhere.

Four sites—two located relatively near the point of Mississippi River inundation (near sites) and two located relatively far from the inundation point (far sites)—were haphazardly chosen as representative floodplain habitats (e.g., areas experiencing a moving littoral edge) across a gradient of decreasing hydrologic connectivity (Figure 1). The qualitative designations of "near" and "far" correspond to respective relative distances from the initial inundation point by the Mississippi River at the rock weir in the southern portion of the WMA (Figure 1). Near sites (approximately 2.75- and 3.00-km straight-line distances to the rock weir)

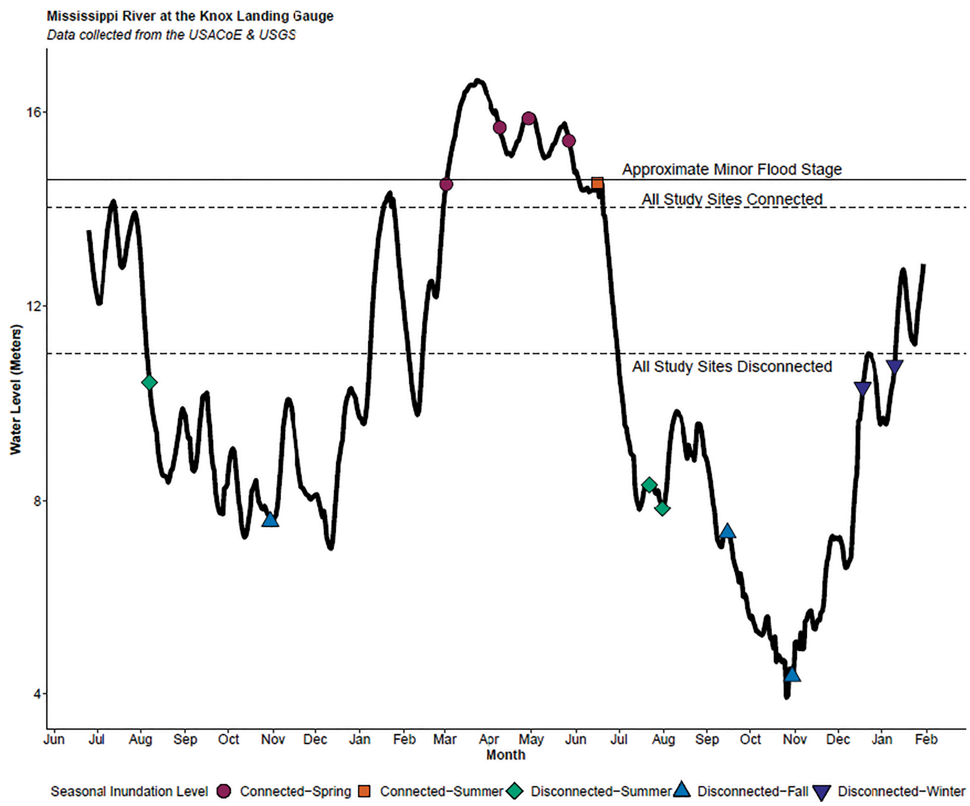


**Figure 2.** Hydrograph representing the timeline of sampling from August 7, 2021, to January 20, 2023. Approximate levels of inundation experienced at the Richard K. Yancey Wildlife Management Area are represented by dashed lines. Minor flood stage of the Mississippi River is represented by the solid line. Data are from the U.S. Army Corps of Engineers (USACOE) and U.S. Geological Survey (USGS).

consistently receive more frequent inundation than the far sites via the flood pulse beginning in early spring. Conversely, the far sites (approximately 6.2- and 8.6-km straight-line distances to the rock weir) require higher spring river stages to become connected to the main stem compared to the near sites (Figure 2). For the flood pulse to reach the far sites, water must over-top natural and anthropogenic barriers between the near and far sites. When the floodplain is dewatered, low elevation at all four sites retains water between flood events. The 13 sampling days were first categorized by floodplain inundation level and then by season: connected–spring (March 2, April 9, April 29, and May 27, 2022), connected–summer (June 16, 2022), disconnected–summer (August 7, 2021; July 22 and July 30, 2022), disconnected–fall (October 30, 2021; September 15 and October 30, 2022), and disconnected–winter (December 18, 2022; January 10, 2023). Only one connected–summer day was sampled (June 16, 2022) due to rapid dewatering of the floodplain. The July 22, 2022, sampling event was abbreviated due to mechanical failure of the sonar power source; however, one near site and one far site were successfully sampled. "Connected" was defined as all four sites being simultaneously inundated by Mississippi River floodwaters. "Disconnected" refers to when all four sites were hydrologically separated from the Mississippi River. The categorical inundation levels were determined by Knox River Landing gauge measurements (U.S. Army Corps of Engineers and U.S. Geological Survey station 07294800; https://waterdata.usgs.gov/monitoring-location/07294800/#parameterCode=00065&period=P7D) and from visual observations at the sites.

## Data collection

An ARIS Explorer 3000 (hereafter, ARIS), operating at a maximum of 3 MHz, was secured to a weighted polyethylene platform (33 × 33 × 28 cm) and manually deployed from a stationary position within 1 m of the bank, resting on the bottom of the floodplain. The sonar was positioned perpendicular to the water column to minimize interference from the surface or bottom of the floodplain. Sites were greater than the 20-m maximum range of the ARIS; therefore, a range of approximately 8 m was selected to achieve higher resolution. The ARIS recorded at a rate of approximately 10 frames/s with a 30° × 14° field of view. The sonar and platform were manually repositioned 90° every 20 min to increase coverage of the floodplain. As such, each site was recorded for approximately 1 h in a near 270° view of the floodplain, excluding the area behind the sonar that faced the bank. Sampling at each of the four sites occurred on each sample date between sunrise (approximately 0630 hours) and sunset (approximately 1730 hours), except on July 22, 2022, when only two sites were sampled due to equipment failure. Site order was randomly determined for each sampling prior to ARIS deployment. During each deployment and rotation, organisms were given 5 min to acclimate before recording was initiated.

## Quantification of gar abundance and size-class distribution

Relative fish abundance (i.e., total number) was estimated using the maximum number recorded (Max*N*) method as described by Cappo et al. (2004). Previous research has used

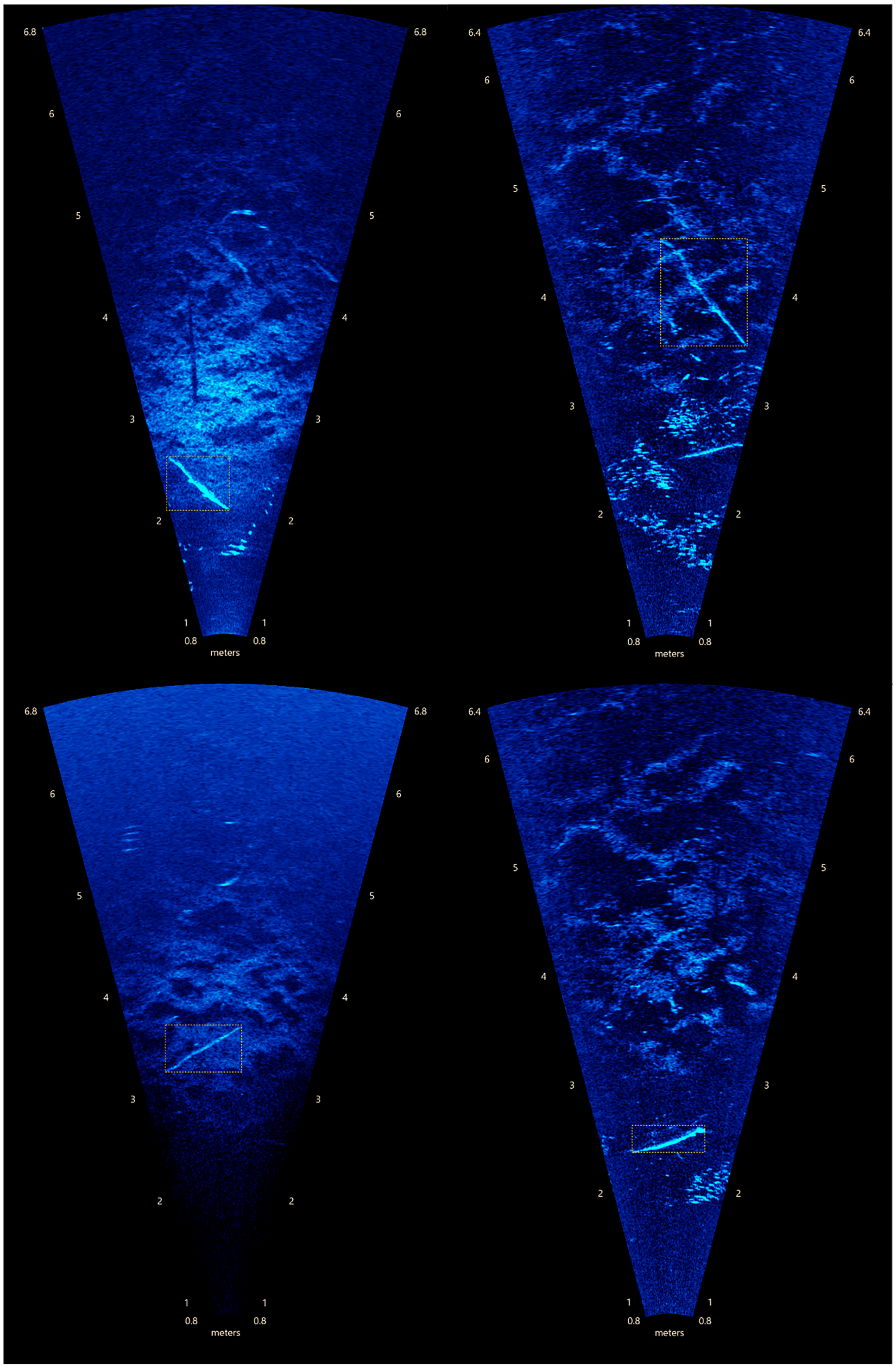


**Figure 3.** Examples of high-resolution video data from the ARIS Explorer 3000. Dashed boxes indicate perpendicularly oriented gar that were measured using ARIS Fish software.

the Max*N* method to estimate fish abundance from data collected via high-resolution imaging sonars (Becker et al., 2011, 2013; Cappo et al., 2007; Rieucau et al., 2015). To include the total number of fish present, we counted the total number of gar observed in the ARIS field of view in all recorded frames (individual gar leaving the field of view and later coming back were counted as new individuals). All gar present in a given frame were counted regardless of size or behavior.

Using ARISFish software (Sound Metrics Corporation), we manually measured the total body lengths (m) of individual gar that were oriented approximately perpendicular to the sonar lens. This procedure minimizes error in obtaining total body length estimates via sonar (Becker et al., 2011). The elongated, fast-start predator body shape and the caudal fin swimming style allow gar to be readily identified in ARIS footage (Figure 3). However, identification of gar to the species level remains a challenge unless the individual is greater than 0.80 m. Beyond this size threshold, morphological features, such as the longer snout of a Longnose Gar or the stockier body of an Alligator Gar, are apparent. Therefore, the following gar size-classes were used to capture generalized life stages (i.e., young of the year, juvenile, subadult, and adult) to explain ecological function and relevance of floodplain habitat use: 0.20–0.40 m, 0.41–0.60 m, 0.61–0.80 m, 0.81–1.00 m, and 1.01 m and greater. The number of size-classes is different from the number of life stages because of size variation across species.

### Statistical analysis

Observations (i.e., counts) of gar in each size-class were recorded for each site (near 1, near 2, far 1, and far 2) and the corresponding seasonal inundation level (i.e., connected–spring, disconnected–summer, etc.). Means and SEs were calculated while maintaining the independence of each site to achieve greater precision than would have been possible if sites were pooled. For the two largest size-classes, in which species identification was possible, counts are provided for each species identified in lieu of statistical analyses due to low sample sizes. Pearson's chi-square test was used to examine whether gar detections (i.e., counts), regardless of size-class, via imaging sonar monitoring differed between the floodplain connectivity variables of seasonal inundation level and proximity to the inundation point. This procedure was used to test the null hypothesis that gar detections at near and far sites did not vary among seasonal inundation levels. Multivariate techniques were used to assess spatiotemporal patterns in abundance and size-class distribution on each size-class simultaneously to minimize type I error rates from individual univariate analyses. Data were not transformed prior to multivariate analyses. Nonmetric multidimensional scaling (NMDS) with the Bray–Curtis dissimilarity matrix was used to visualize dissimilarities in a reduced dimensional space via the metaMDS function of the vegan package in R (R Foundation for Statistical Computing; www.r-project.org), with 10,000 permutations. Five NMDS ordinations were created and compared for appropriate stress values ($k < 0.10$). Plots grouped the samples (i.e., combinations of date, site, and proximity to the Mississippi River) based on the seasonal inundation level. Patterns were further analyzed using permutational multivariate ANOVA (PERMANOVA) with the Bray–Curtis dissimilarity matrix from the vegan package in R, with 10,000 permutations. This procedure was used to test the null hypothesis that there were no differences in the relative abundance and distribution of size-classes among seasonal inundation levels, proximity to the Mississippi River, or their interaction. Permutational pairwise comparisons were made using the RVAideMemoire package in R, with 10,000 permutations. All analyses were performed using R version 4.2.2.

## RESULTS

We collected 56 h of video footage from August 7, 2021, to January 10, 2023, that included 273 gar observations (Table 1). For the two largest size-classes, in which species identification based on morphological characteristics was reliable, 21 gar were observed, with 17 identified as Longnose Gar and four identified as Alligator Gar. During disconnected–summer,

**Table 1.** Maximum number of gar recorded (*n* gar) and average (±SE) number of gar by size-class from four sites on the Richard K. Yancy Wildlife Management Area, Louisiana, with respect to seasonal inundation level and proximity to the point of Mississippi River inundation (near sites or far sites). Means and SEs were calculated without combining sites, thus maintaining distinctions based on site location and seasonal inundation level.

| | Near sites | | Far sites | |
|---|---|---|---|---|
| **Inundation–season and gar size-class (m)** | ***n* gar** | **Average *n* gar ± SE** | ***n* gar** | **Average *n* gar ± SE** |
| **Connected–spring** | | | | |
| **0.20–0.40** | 2 | 0.25 ± 0.16 | 6 | 0.75 ± 0.53 |
| **0.41–0.60** | 1 | 0.13 ± 0.13 | 10 | 1.25 ± 0.73 |
| **0.61–0.80** | 5 | 0.63 ± 0.18 | 5 | 0.63 ± 0.26 |
| **0.81–1.00** | 0 | 0 | 3 | 0.38 ± 0.26 |
| **>1.01** | 0 | 0 | 2 | 0.25 ± 0.25 |
| **Connected–summer** | | | | |
| **0.20–0.40** | 9 | 4.50 ± 4.50 | 7 | 3.50 ± 0.50 |
| **0.41–0.60** | 7 | 3.50 ± 2.50 | 3 | 1.50 ± 1.50 |
| **0.61–0.80** | 1 | 0.50 ± 0.50 | 1 | 0.50 ± 0.50 |
| **0.81–1.00** | 1 | 0.50 ± 0.50 | 0 | 0 |
| **>1.01** | 0 | 0 | 0 | 0 |
| **Disconnected–summer** | | | | |
| **0.20–0.40** | 16 | 3.20 ± 1.74 | 8 | 1.60 ± 0.60 |
| **0.41–0.60** | 32 | 6.4 ± 2.18 | 9 | 1.8 ± 0.86 |
| **0.61–0.80** | 42 | 8.40 ± 2.89 | 8 | 1.60 ± 0.40 |
| **0.81–1.00** | 12 | 2.40 ± 1.03 | 0 | 0 |
| **>1.01** | 0 | 0 | 1 | 0.20 ± 0.20 |
| **Disconnected–fall** | | | | |
| **0.20–0.40** | 1 | 0.17 ± 0.17 | 7 | 1.67 ± 0.48 |
| **0.41–0.60** | 12 | 2.00 ± 0.68 | 15 | 2.50 ± 0.67 |
| **0.61–0.80** | 15 | 2.50 ± 1.26 | 6 | 1.00 ± 0.45 |
| **0.81–1.00** | 1 | 0.17 ± 0.17 | 1 | 0.17 ± 0.17 |
| **>1.01** | 0 | 0 | 0 | 0 |
| **Disconnected–winter** | | | | |
| **0.20–0.40** | 0 | 0 | 0 | 0 |
| **0.41–0.60** | 8 | 2.00 ± 1.68 | 6 | 1.50 ± 1.19 |
| **0.61–0.80** | 4 | 1.00 ± 0.71 | 6 | 1.50 ± 0.87 |
| **0.81–1.00** | 0 | 0 | 0 | 0 |
| **>1.01** | 0 | 0 | 0 | 0 |

eight Longnose Gar and four Alligator Gar were detected at near sites and one Longnose Gar was detected at a far site. During disconnected–fall, two Longnose Gar were observed at both near and far sites. Five Longnose Gar were observed at far sites only during connected–spring, and one Longnose Gar was found during disconnected–summer. No Longnose Gar in the two largest size-classes were detected during disconnected–winter. In addition, Alligator Gar greater than 0.81 m were not detected during connected–spring, connected–summer, disconnected–fall, or disconnected–winter.

The chi-square test indicated ($\chi^2 = 43.32$, df = 4, $P < 0.0001$) that detections of gar (i.e., counts) via imaging sonar monitoring differed between the floodplain connectivity variables of seasonal inundation level and proximity to the Mississippi River (Figure 4). This relationship was driven by disconnected–summer periods at near sites, accounting for approximately 37% of all gar detections (Figure 4; Table 1). The pattern was driven by two size-classes (0.41–0.60 and 0.61–0.80 m) that accounted for 74 of the 102 gar detected during disconnected–summer periods at near sites (Figure 4; Table 1). At near sites

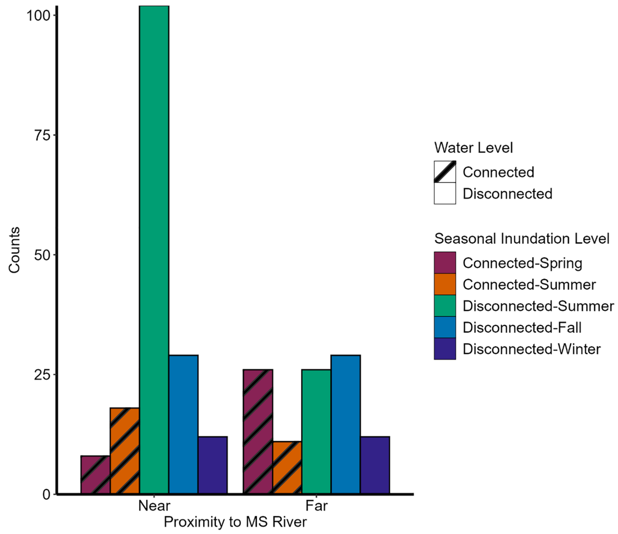


**Figure 4.** Bar plot depicting the results of the chi-square analysis comparing seasonal inundation level and site proximity to the initial inundation point of Mississippi (MS) River floodwaters. The *y*-axis represents the counts of gar for each inundation level and season category.

during disconnected–summer, the mean ± SE number of gar in the 0.41–0.60-m size-class was 6.4 ± 2.18 and the number of gar in the 0.61–0.80-m size-class was 8.40 ± 2.89. Comparatively, at far sites during disconnected–summer, the mean ± SE number of gar in the 0.41–0.60-m size-class was 1.8 ± 0.86 and the number of gar in the 0.61–0.80-m size-class was 1.60 ± 0.40 (Table 1). Despite the greater number of detections of gar in these size-classes at near sites during disconnected–summer, gar observations were also more sporadic and included several instances when no gar were recorded via imaging sonar monitoring.

The NMDS revealed notable monotonic relationships among gar size-classes and the NMDS dimensions (Figure 5). Size-class distribution of gar differed (df = 4, $R^2 = 0.25$, $P < 0.0001$), with the PERMANOVA model suggesting that seasonal inundation level in the WMA was the only significant factor (Figure 5; Table 2). Permutational pairwise comparisons indicated that dissimilar distributions of gar size-classes occurred between connected–spring and disconnected–fall ($P = 0.039$; Table 3), likely driven by the 0.41–0.60-m and 0.61–0.80-m size-classes due to the tendency to group closer to the disconnected–fall sampling events in the NMDS (Figure 5; Table 1). A trend was detected between connected–spring and disconnected–summer ($P = 0.070$; Table 3), again driven by the 0.41–0.60-m and 0.61–0.80-m size-classes and, to a lesser extent, the 0.20–0.40-m size-class (Figure 5; Table 1). Comparisons between other seasonal inundation levels were nonsignificant (Table 3).

## DISCUSSION

Our study demonstrates that the use of floodplain habitats by the gar assemblage was affected by the degree of Mississippi River–floodplain connectivity. We found that the seasonal inundation level and proximity to the point of inundation by the Mississippi River influenced gar abundance. As revealed by the chi-square analysis, approximately 37% of all gar detections occurred at near sites during disconnected–summer, suggesting that gar were most abundant when the floodplain had recently dewatered. This observation of higher relative abundance of gar at near sites during disconnected–summer periods was driven by more detections of the 0.41–0.60-m and 0.61–0.80-m size-classes. However, the NMDS and PERMANOVA suggested that the distribution of size-classes was explained by the seasonal inundation level alone. Contrary to the abundance results, the two most numerous size-classes did not cluster in the same region of multidimensional space as disconnected–summer periods, but they tended to group in the same regions as disconnected–fall periods. A likely explanation for this discrepancy lies in the consistency of detections during each period. Although the 0.41–0.60-m and 0.61–0.80-m size-classes were most numerous during disconnected–summer, this occurred only at the near sites and included sampling days when no gar were detected, followed by sampling days in which detections were numerous. In contrast, during the disconnected–fall, these two size-classes were consistently detected across both near and far sites, accounting for approximately 17% of all gar detections.

It could be argued that the patterns of gar abundance observed across seasonal inundation levels were influenced by a combination of changing gar density and movement patterns due to fluctuating water levels. Although the volume of water sampled during our acoustic monitoring remained the same across inundation levels, higher water levels during connected periods may have allowed gar to access habitats that were outside our sonar's field of view. In contrast, while low-water periods may confine gar to smaller bodies of water (Bonvillain et al., 2008), the patterns observed for the 0.41–0.60-m and 0.61–0.80-m size-classes are unlikely to reflect changes in density or restricted movement due to concentration effects. Even during disconnected periods, the monitored sites were large enough for gar to move freely within habitats, suggesting that habitat restriction could not solely explain the abundance patterns reported in our study. Future efforts should consider extending the imaging sonar coverage, thereby increasing the volume of water monitored and alleviating concerns about the field of view. Despite these limitations, observed patterns emphasized by the 0.41–0.60-m and 0.61–0.80-m size-classes underscore the importance of low-water floodplain refuges that enable gar to persist between connected inundation periods.

We anticipate that all four gar species native to Louisiana occur within the monitored sections of the Richard K. Yancey WMA. The four native gar species in Louisiana have been speculated to separate in response to available habitats within the floodplain, such as Alligator Gar and Longnose Gar being more abundant near the river and the other species inhabiting distant floodplain habitats year-round (Robertson et al., 2008). However, other work suggests a relatively strong co-occurrence of Longnose Gar and Shortnose Gar, mediated by the proximity of a floodplain lake to a river and lake latitude (Schumann et al., 2020). Occurrence patterns of Spotted Gar are independent of the other species, given this species' ubiquity in southeastern floodplains (Schumann et al., 2020). In our study, morphological differences among the four native gar species in Louisiana were not easily distinguishable from the ARIS footage unless the focal individual was greater than 0.80 m. A

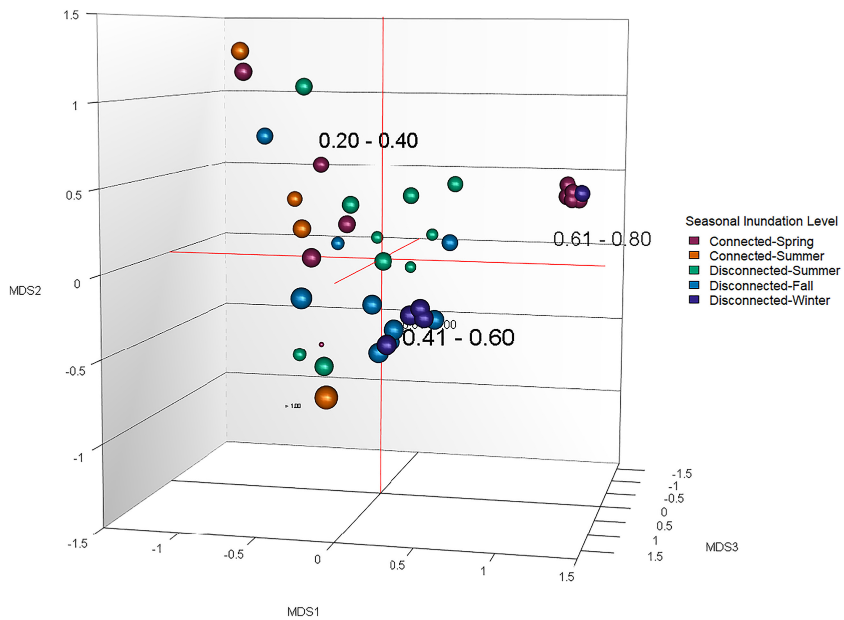


**Figure 5.** Nonmetric multidimensional scaling ordination ($k=3$; stress = 0.043) of the gar size-class distribution. Spheres represent individual sampling events grouped by the seasonal inundation level, as tested within the permutational multivariate ANOVA ($R^2=0.28$, $P=0.0015$). Sizes of spheres and size-class labels correspond to the depth of field, where larger spheres or text are more positive with respect to the third multidimensional scaling (MDS3) axis and smaller spheres or text are more negative with respect to the MDS3 axis. Spheres have been slightly spread to prevent overlap. Solid lines are centered at 0, 0 in the respective *x*, *y*, and *z* planes. Data used were counts for each gar size-class from recorded ARIS footage of the Richard K. Yancey Wildlife Management Area. Untransformed data with a Bray–Curtis dissimilarity matrix and 10,000 permutations were used for the analysis.

**Table 2.** Results of the permutational multivariate ANOVA with seasonal inundation level as the single explanatory variable following model parsimony. Untransformed gar abundance data with a Bray–Curtis dissimilarity matrix and 10,000 permutations were used for the analysis.

| Source of variation | df | Sum of squares | $R^2$ | $F$ | Pr(>$F$) |
|---|---|---|---|---|---|
| **Inundation–season** | 5 | 2.2501 | 0.27828 | 2.5448 | 0.0015 |
| **Residual** | 33 | 5.8356 | 0.72172 | – | – |
| **Total** | 38 | 8.0856 | 1.00000 | – | – |

current challenge inherent to imaging sonar technology is the limited species-level taxonomic resolution (see Munnelly et al., 2023). To overcome this limitation, we grouped individuals into five size-classes. Given that habitat features (i.e., floodplain lakes and proximity to the main channel) known to drive co-occurrence are available within the WMA, we proceed under the assumption that all four species occurred, and we discuss the most likely taxonomic composition of each size-class with regard to responses to predation, foraging, and reproduction.

All four gar species in the 0.20–0.40-m size-class were expected to be young-of-the-year/juvenile/subadult individuals (Kelley, 2012; Ladonski, 1998; McGrath, 2010; Smylie et al., 2016), with a noteworthy exception being Spotted Gar and Shortnose Gar males, which can reach maturity in this size-class (Smith, 2008). Gar in the 0.20–0.40-m size-class likely remain on the floodplain year-round to access foraging opportunities, feeding on macroinvertebrate (Bonvillain & Fontenot, 2020; Snow et al., 2020) and fish prey (Robertson et al., 2008). The gar in the 0.20–0.40-m size-class are subject to predation pressure from American alligators *Alligator mississippiensis* and piscivorous birds (Valentine et al., 1972). Disconnected–summer and disconnected–fall samples tended to cluster in the same region as the 0.20–0.40-m size-class, possibly due to the difficulty in observing this size-class during connected–spring and connected–summer. Based on previous studies, this size-class remains in or near submerged vegetation during high water to maximize foraging success and reduce predation (Brinkman & Fisher, 2019; Eschelle & Riggs, 1972; McAllister et al., 2023).

Similarly, all four gar species would be expected in the 0.41–0.60-m and 0.61–0.80-m size-classes. Adult Spotted, Shortnose, and Longnose gars and juvenile Alligator Gar would be in both size-classes, with a few juvenile Longnose Gar occurring in the 0.41–0.60-m size-class (Ferrara, 2001; Ladonski, 1998; McGrath, 2010; Smith, 2008; Smylie et al., 2016). Both size-classes access inundated floodplains for foraging and spawning opportunities, a pattern that has been observed in previous studies (Ferrara, 2001; Smylie et al., 2016). Most samples from disconnected–fall were observed in the same region of multidimensional space as these two size-classes, suggesting that these size-classes may remain in the floodplain past the dewatering phase.

In the 0.81–1.00-m size-class, adult Longnose Gar and juvenile Alligator Gar are present, with fewer adult Spotted Gar and Shortnose Gar expected (Felterman, 2015; Ferrara, 2001; Johnson & Noltie, 1997; Kelley, 2012; McGrath, 2010). Any gar in the largest size-class (>1.01 m) are expected to be adult or juvenile Alligator Gar or adult Longnose Gar (Felterman, 2015; Ferrara, 2001; Johnson & Noltie, 1997; Kelley, 2012). Only 8% of our observations included the two largest size-classes: 18 gar were observed in the 0.81–1.00-m size-class, and three individuals were observed in the >1.01-m size-class. The majority of these

**Table 3.** Summary of pairwise comparisons using permutational multivariate ANOVA on a Bray–Curtis distance matrix, with the false discovery rate adjusted.

| Inundation–season | Connected–spring | Connected–summer | Disconnected–summer | Disconnected–fall |
|---|---|---|---|---|
| **Connected–summer** | 0.093 | – | – | – |
| **Disconnected–summer** | 0.070 | 0.172 | – | – |
| **Disconnected–fall** | 0.039 | 0.093 | 0.166 | – |
| **Disconnected–winter** | 0.402 | 0.093 | 0.093 | 0.085 |

observations (17 of 21 gar) were confirmed to be Longnose Gar by a narrow, elongated snout. The remaining were confirmed to be Alligator Gar, exhibiting stout bodies and thicker snouts. A greater proportion of gar in the 0.81–1.00-m size-class were observed during disconnected–summer at near sites. The three gar in the largest size-class were observed at far sites during connected–spring and disconnected–summer. This supports the idea that adult Longnose Gar and adult/juvenile Alligator Gar traverse far into the floodplain to access formerly inaccessible areas (Ferrara, 2001; Robertson et al., 2008; Wegener et al., 2017). Dewatering of the floodplain has been associated with the emigration of Longnose Gar and Alligator Gar toward deepwater habitats nearer to the main channel (Buckmeier et al., 2013; Kluender et al., 2016). Near sites remained inundated for longer periods and could serve as low-water habitats for larger individuals (Roberston et al., 2008; Wegener et al., 2017). However, given the rapid dewatering that occurred in mid to late summer 2022, a plausible explanation for observing these size-classes on the floodplain at low water is that individuals were unable to leave the interior floodplain before the floodwaters receded below natural and anthropogenic barriers.

Altogether, our results suggest that remaining pools of water, when disconnected from the main-stem river, may provide both nursery and refuge habitats to floodplain-associated gar with body lengths between 0.20 and 0.80 m. Low-water refuge may impede the access of larger conspecifics or interspecific competitors, thereby releasing smaller gar from predation (Bănăduc et al., 2021; Magoulick & Kobza, 2003; Richard et al., 2018) and reducing resource competition (Correa & Winemiller, 2014; Echelle & Riggs, 1972; Kovalenko, 2019; Snow et al., 2020). No gar smaller than 0.20 m was detected, but given the life histories of gar, this is not unexpected. Mature female gar use nearshore submerged aquatic vegetation and substrate during the flood pulse for egg deposition (Inebnit, 2009). Upon hatching, young-of-the-year gar remain attached to vegetation for several days until they eventually become free-swimming (Buckmeier et al., 2017; Inebnit, 2009; Mendoza et al., 2002). Young-of-the-year gar stay in or near submerged aquatic vegetation to avoid predation by larger conspecifics or other piscivorous fishes (Eschelle & Riggs, 1972; McAllister et al., 2023). Sonar deployment tended to occur near mudflats or mowed batture grasslands that, once inundated, are likely unsuitable for hatching/young-of-the-year gar. Fortunately, modern imaging sonars are now capable of detecting objects as small as 4 mm; therefore, targeted sampling of highly vegetated areas during and immediately after the spawning period may alleviate this issue in the future.

Our results demonstrate that gar abundance and size-class distribution are influenced by floodplain connectivity, suggesting that the planned restoration efforts in this area may have measurable effects on the gar assemblage. Enhancing hydrologic connectivity may provide more consistent access to critical foraging and spawning habitats while reducing the isolation of gar to smaller water bodies outside of the flood pulse (Roberts et al., 2023). As restoration progresses, future research should focus on monitoring how increased connectivity impacts the gar assemblage and using imaging sonar to monitor gar passage through the newly installed culverts. Additionally, imaging sonar monitoring may help to validate geospatial models, like those by Allen et al. (2020) and Meitzen et al. (2023), that identify critical gar habitat. However, species-level identification remains a challenge inherent to imaging sonar data sets (Munnelly et al., 2023), emphasizing the continued need for traditional direct-capture techniques (e.g., electrofishing, gill nets, and jug lines) to effectively identify species and determine species-specific size-class structure (Colvin, 2002; McInerny & Cross, 2004; Seidensticker & Ott, 1988). Future research should also explore previously difficult questions, such as detecting individuals under 0.20 m, understanding trophic interactions, and observing reproductive behaviors with minimal disturbance. We anticipate that our study, alongside the increasing use of imaging sonar technology, will inform and improve future management actions and conservation strategies for gar populations.

## DATA AVAILABILITY

The data collected and analyzed during our study are available upon reasonable request.

## ETHICS STATEMENT

No capture or handling of animals was conducted in our study, as it was solely based on nonintrusive observations.

## FUNDING

This project was funded through National Fish and Wildlife Foundation grant #67600 to G.R.

## CONFLICTS OF INTEREST

None declared.

## ACKNOWLEDGMENTS

We are grateful to the two anonymous reviewers for providing constructive comments and critiques, which we believe strengthened the manuscript. We thank the Richard K. Yancey WMA staff for their assistance and hospitality. We thank Raynie Harlan for guidance and stewardship. We also extend our thanks to Ashleigh Lambiotte, Brianna Jordan, Erica Teschke, Leflore James Press, and Franchesca Basalo for assistance in the field and laboratory. We appreciate Dr. Lucas James Kirschman and Dr. Jonathan Willis for providing additional support.

## REFERENCES

Alford, J. B., & Walker, M. R. (2013). Managing the flood pulse for optimal fisheries production in the Atchafalaya River basin, Louisiana (USA). *River Research and Applications*, *29*, 279–296. https://doi.org/10.1002/rra.1610

Allen, Y., Kimmel, K., & Constant, G. (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. https://doi.org/10.1002/nafm.10433

Arthington, A. H., Balcombe, S. R., Wilson, G. A., Thoms, M. C., & Marshall, J. (2005). Spatial and temporal variation in fish-assemblage structure in isolated waterholes during the 2001 dry season of an arid-zone floodplain river, Cooper Creek, Australia. *Marine & Freshwater Research*, *56*, 25–35. https://doi.org/10.1071/MF04111

Bănăduc, D., Sas, A., Cianfaglione, K., Barinova, S., & Curtean-Bănăduc, A. (2021). The role of aquatic refuge habitats for fish, and threats in the context of climate change and human impact, during seasonal hydrological drought in the Saxon Villages area (Transylvania, Romania). *Atmosphere*, *12*, Article 1209. https://doi.org/10.3390/atmos12091209.

Baustian, J. J., Piazza, B. P., & Bergan, J. F. (2019). Hydrologic connectivity and backswamp water quality during a flood in the Atchafalaya basin, USA. *River Research and Applications*, *35*, 430–435. https://doi.org/10.1002/rra.3417

Bayley, P. B. (1995). Understanding large river–floodplain ecosystems. *BioScience*, *45*, 153–158. https://doi.org/10.2307/1312554

Becker, A., Cowley, P. D., Whitfield, A. K., Järnegren, J., & Næsje, T. F. (2011). Diel fish movements in the littoral zone of a temporarily closed South African estuary. *Journal of Experimental Marine Biology and Ecology*, *406*, 63–70. https://doi.org/10.1016/j.jembe.2011.06.014

Becker, A., Whitfield, A. K., Cowley, P. D., Järnegren, J., & Næsje, T. F. (2013). Potential effects of artificial light associated with anthropogenic infrastructure on the abundance and foraging behaviour of estuary-associated fishes. *Journal of Applied Ecology*, *50*, 43–50. https://doi.org/10.1111/1365-2664.12024

Benevides, L. J., Cardozo-Ferreira, G. C., Ferreira, C. E. L., Pereira, P. H. C., Pinto, T. K., & Sampaio, C. L. S. (2019). Fear-induced behavioural modifications in damselfishes can be diver-triggered. *Journal of Experimental Marine Biology and Ecology*, *514–515*, 34–40. https://doi.org/10.1016/j.jembe.2019.03.009

Bennett, D. L., Ott, R. A., & Bonds, C. C. (2015). Surveys of Texas bow anglers, with implications for managing Alligator Gar. *Journal of the Southeastern Association of Fish and Wildlife Agencies*, *2*, 8–14.

Bonvillain, C. P., Ferrara, A. M., & Fontenot, Q. C. (2008). Relative abundance and biomass estimate of a Spotted Gar population in a seasonally connected large river floodplain lake. *Journal of the Southeastern Association of Fish and Wildlife Agencies*, *62*, 177–182.

Bonvillain, C. P., & Fontenot, Q. C. (2020). The annual flood pulse mediates crayfish as a major diet constituent of carnivorous fishes in south Louisiana. *Freshwater Crayfish*, *25*, 69–75. https://doi.org/10.5869/fc.2020.v25-1.069

Braasch, I., Gehrke, A. R., Smith, J. J., Kawasaki, K., Manousaki, T., Pasquier, J., Amores, A., Desvignes, T., Batzel, P., Catchen, J., Berlin, A. M., Campbell, M. S., Barrell, D., Martin, K. J., Mulley, J. F., Ravi, V., Lee, A. P., Nakamura, T., Chalopin, D., … Postlethwait, J. H. (2016). The Spotted Gar genome illuminates vertebrate evolution and facilitates human–teleost comparisons. *Nature Genetics*, *48*, 427–437. https://doi.org/10.1038/ng.3526

Brinkman, E. L., & Fisher, W. L. (2019). Life history characteristics of Alligator Gar (*Atractosteus spatula*) in the upper Red River (Oklahoma–Texas). *The Southwestern Naturalist*, *64*, 98–108. https://doi.org/10.1894/0038-4909-64-2-98

Buckmeier, D. L., & Schlechte, J. W. (2009). Capture efficiency and size selectivity of Channel Catfish and Blue Catfish sampling gears. *North American Journal of Fisheries Management*, *29*, 404–416. https://doi.org/10.1577/M08-136.1

Buckmeier, D. L., Smith, N. G., & Daugherty, D. J. (2013). Alligator Gar movement and macrohabitat use in the lower Trinity River, Texas. *Transactions of the American Fisheries Society*, *142*, 1025–1035. https://doi.org/10.1080/00028487.2013.797494

Buckmeier, D. L., Smith, N. G., Daugherty, D. J., & Bennett, D. L. (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.

Buckmeier, D. L., Smith, N. G., Schlechte, J. W., Ferrara, A. M., & Kirkland, K. (2016). Size structure, population abundance, and angler exploitation. *Journal of the Southeastern Association of Fish and Wildlife Agencies*, *3*, 33–38.

Burdis, R. M., DeLain, S. A., Lund, E. M., Moore, M. J. C., & Popp, W. A. (2020). Decadal trends and ecological shifts in backwater lakes of a large floodplain river: Upper Mississippi River. *Aquatic Sciences*, *82*, Article 27. https://doi.org/10.1007/s00027-020-0703-7

Butler, S. E., Einfalt, L. M., Abushweka, A. A., & Wahl, D. H. (2018). Ontogenetic shifts in prey selection and foraging behaviour of larval and early juvenile Alligator Gar (*Atractosteus spatula*). *Ecology of Freshwater Fish*, *28*, 385–395. https://doi.org/10.1111/eff.12461

Cappo, M., De'ath, G., & Speare, P. (2007). Inter-reef vertebrate communities of the Great Barrier Reef Marine Park determined by baited remote underwater video stations. *Marine Ecology Progress Series*, *350*, 209–221. https://doi.org/10.3354/meps07189

Cappo, M., Speare, P., & De'ath, G. (2004). Comparison of baited remote underwater video stations (BRUVS) and prawn (shrimp) trawls for assessments of fish biodiversity in inter-reefal areas of the Great Barrier Reef Marine Park. *Journal of Experimental Marine Biology and Ecology*, *302*, 123–152. https://doi.org/10.1016/j.jembe.2003.10.006

Colvin, M. A. (2002). A comparison of gill netting and electrofishing as sampling techniques for White Bass in Missouri's large reservoirs. *North American Journal of Fisheries Management*, *22*, 690–702. https://doi.org/10.1577/1548-8675(2002)022<0690:ACOGNA>2.0.CO;2

Correa, S. B., & Winemiller, K. (2014). Niche partitioning among frugivorous fishes in response to fluctuating resources in the Amazonian floodplain forest. *Ecology*, *95*, 210–224. https://doi.org/10.1890/13-0393.1

David, S. R., King, S. M., & Stein, J. A. (2018). Introduction to a special section: Angling for dinosaurs—Status and future study of the ecology, conservation, and management of ancient fishes. *Transactions of the American Fisheries Society*, *147*, 623–625. https://doi.org/10.1002/tafs.10072

Echelle, A. A., & Riggs, C. D. (1972). Aspects of the early life history of gars (*Lepisosteus*) in Lake Texoma. *Transactions of the American Fisheries Society*, *101*, 106–112. https://doi.org/10.1577/1548-8659(1972)101<106:AOTELH>2.0.CO;2

Eggleton, M. A., Fontenot, Q. C., & Jackson, J. R. (2016). The lower Mississippi River floodplain ecosystem: Current status and future potential introduction. In Y. Chen, D. Chapman, J. Jackson, D. Chen, Z. Li, K. Killgore, & Q. Phelps (Eds.), *Fishery resources, environment, and conservation in the Mississippi and Yangtze River basins* (pp. 235–262). American Fisheries Society. https://doi.org/10.47886/9781934874448.ch12

Felterman, M. A. (2015). *Population dynamics, reproductive biology and diet of Alligator Gar* Atractosteus spatula *in Terrebonne estuary and Rockefeller Wildlife Refuge* [Unpublished master's thesis]. Nicholls State University.

Ferrara, A. M. (2001). *Life-history strategy of Lepisosteidae: Implications for the conservation and management of Alligator Gar* [Doctoral dissertation, Auburn University]. ProQuest Dissertations & Theses.

Gilbert, D. J., McKenzie, J. R., & Davies, N. M. (2001). Evidence from tag recapture experiments that fish learn to avoid fishing gear. *Journal of Agricultural, Biological, and Environmental Statistics*, *6*, 281–291. https://doi.org/10.1198/108571101750524779

Inebnit, T. E., III. (2009). *Aspects of the reproductive and juvenile ecology of Alligator Gar in the Fourche LaFave River, Arkansas* [Unpublished master's thesis]. University of Central Arkansas.

Jenney, C. J., Nemec, Z. C., Lee, L. N., & Bonar, S. A. (2022). Increased juvenile native fish abundance following a major flood in an Arizona river. *Journal of Freshwater Ecology*, *37*, 1–14. https://doi.org/10.1080/02705060.2021.2002734

Johnson, B. L., & Noltie, D. B. (1997). Demography, growth, and reproductive allocation in stream-spawning Longnose Gar. *Transactions of the American Fisheries Society*, *126*, 438–466. https://doi.org/10.1577/1548-8659(1997)126<0438:DGARAI>2.3.CO;2

Junk, W. J., Bayley, P. B., & Sparks, R. E. (1989). The flood pulse concept in river–floodplain systems. In D. P. Dodge (Ed.), *Proceedings of the international large river symposium* (pp. 110–127). Department of Fisheries and Oceans Canada.

Kelley, S. W. (2012). Age and growth of spawning Longnose Gar (*Lepisosteus osseus*) in a north central Texas reservoir. *Western North American Naturalist*, *72*, 69–77. https://doi.org/10.3398/064.072.0108

Kemp, G. P., Day, J. W., & Freeman, A. M. (2014). Restoring the sustainability of the Mississippi River delta. *Ecological Engineering*, *65*, 131–146. https://doi.org/10.1016/j.ecoleng.2013.09.055

King, A. J., Tonkin, Z., & Mahoney, J. (2009). Environmental flow enhances native fish spawning and recruitment in the Murray River, Australia. *River Research and Applications*, *25*, 1205–1218. https://doi.org/10.1002/rra.1209

Kluender, E. R., Adams, R., & Lewis, L. (2016). Seasonal habitat use of Alligator Gar in a river–floodplain ecosystem at multiple spatial scales. *Ecology of Freshwater Fish*, *26*, 233–246. https://doi.org/10.1111/eff.12270

Kovalenko, K. E. (2019). Interactions among anthropogenic effects on aquatic food webs. *Hydrobiologia*, *841*, 1–11. https://doi.org/10.1007/s10750-019-04018-x

Ladonski, J. B. (1998). *Life history traits and age-related changes in reproductive potential of the Shortnose Gar* (Lepisosteus platostomus *Rafinesque*) *in southern Illinois* [Unpublished master's thesis]. Southern Illinois University.

Lindholm, M., Hessen, D. O., Mosepele, K., & Wolski, P. (2007). Food webs and energy fluxes on a seasonal floodplain: The influence of flood size. *Wetlands*, *27*, 775–784. https://doi.org/10.1672/0277-5212(2007)27[775:FWAEFO]2.0.CO;2

Lorenzón, R. E., Ronchi-Virgolini, A. L., & Blake, J. G. (2020). Wetland dependency drives temporal turnover of bird species between high- and low-water years in floodplain wetlands of the Paraná River. *Ecohydrology*, *13*, Article e2179. https://doi.org/10.1002/eco.2179

Luo, M., & Criss, R. E. (2018). Increasing stage variability of the Mississippi River. *Journal of Hydrologic Engineering*, *23*, 1–10. https://doi.org/10.1061/(ASCE)HE.1943-5584.0001678

Lyon, J. P., Bird, T., Nicol, S., Kearns, J., O'Mahony, J., Todd, C. R., Cowx, I. G., & Bradshaw, C. J. A. (2014). Efficiency of electrofishing in turbid lowland rivers: Implications for measuring temporal change in fish populations. *Canadian Journal of Fisheries and Aquatic Sciences*, *71*, 878–886. https://doi.org/10.1139/cjfas-2013-0287

Lytle, D. A., & Poff, N. L. R. (2004). Adaptation to natural flow regimes. *Trends in Ecology & Evolution*, *19*, 94–100. https://doi.org/10.1016/j.tree.2003.10.002

Magoulick, D. D., & Kobza, R. M. (2003). The role of refugia for fishes during drought: A review and synthesis. *Freshwater Biology*, *48*, 1186–1198. https://doi.org/10.1046/j.1365-2427.2003.01089.x

McAllister, K., Drake, D. A. R., & Power, M. (2023). Habitat preferences of young-of-year Spotted Gar (*Lepisosteus oculatus*) in Rondeau Bay, Lake Erie. *Canadian Journal of Zoology*, *101*, 1–10. https://doi.org/10.1139/cjz-2022-0081

McCoy, M. M., Sloey, T. M., Howard, R. J., & Hester, M. W. (2020). Response of tidal marsh vegetation to pulsed increases in flooding and nitrogen. *Wetlands Ecology and Management*, *28*, 119–135. https://doi.org/10.1007/s11273-019-09699-8

McGrath, P. E. (2010). *The life history of Longnose Gar,* Lepisosteus osseus, *an apex predator in the tidal waters of Virginia* [Doctoral dissertation, College of William and Mary]. W&M ScholarWorks. https://dx.doi.org/doi:10.25773/v5-y5de-j968

McInerny, M. C., & Cross, T. K. (2004). *Comparison of day electrofishing, night electrofishing, and trap netting for sampling inshore fish in Minnesota lakes*. Minnesota Department of Natural Resources.

Meitzen, K. M., Robertson, C. R., Jensen, J. L., Daugherty, D. J., Hardy, T. B., & Mayes, K. B. (2023). Applying floodplain inundation modeling to estimate suitable spawning habitat and recruitment success for Alligator Gar in the Guadalupe River, Texas. *Hydrology*, *10*, Article 123. https://doi.org/10.3390/hydrology10060123

Mendoza, R., Aguilera, C., Rodríguez, G., González, M., & Castro, R. (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. https://doi.org/10.1023/A:1025047914814

Millar, R. B., & Fryer, R. J. (1999). Estimating the size-selection curves of towed gears, traps, nets and hooks. *Reviews in Fish Biology and Fisheries*, *9*, 89–116. https://doi.org/10.1023/A:1008838220001

Mitsch, W. J., Li, Z., Fink, D. F., Hernandez, M. E., Altor, A. E., Turtle, C. L., & Nahlik, A. M. (2008). Ecological engineering of floodplains. *International Journal of Ecohydrology & Hydrobiology*, *8*, 139–147. https://doi.org/10.2478/v10104-009-0010-3

Mosepele, K., Kolding, J., Bokhutlo, T., Mosepele, B. Q., & Molefe, M. (2022). The Okavango Delta: Fisheries in a fluctuating floodplain system. *Frontiers in Environmental Science*, *10*, Article 854835. https://doi.org/10.3389/fenvs.2022.854835

Munnelly, R. T., Castillo, J. C., Handegard, N. O., Kimball, M. E., Boswell, K. M., & Rieucau, G. (2023). Applications and analytical approaches using imaging sonar for quantifying behavioural interactions among aquatic organisms and their environment. *ICES Journal of Marine Science*, *81*, 207–251. https://doi.org/10.1093/icesjms/fsad182

Narins, P. M., Wilson, M., & Mann, D. A. (2013). Ultrasound detection in fishes and frogs: Discovery and mechanisms. In C. Koppl, G. A. Manley, A. N. Popper, & R. R. Fay (Eds.), *Insights from comparative hearing research* (pp. 135–156). Springer.

Naus, C. J., & Adams, S. R. (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. https://doi.org/10.1111/eff.12319

Nelson, S. A. C., Soranno, P. A., & Qi, J. (2002). Land-cover change in upper Barataria basin estuary, Louisiana, 1972–1992: Increases in wetland area. *Environmental Management*, *29*, 716–727. https://doi.org/10.1007/s00267-001-0060-9

Ochs, C. A., & Shields, F. D. (2019). Fluxes of nutrients and primary production between the main channel and floodplain backwaters of the lower Mississippi River—Development of a simulation model. *River Research and Applications*, *35*, 979–988. https://doi.org/10.1002/rra.3482

Oliveira, I. F., Baccaro, F. B., Werneck, F. P., & Haugaasen, T. (2023). Seasonal flooding decreases fruit-feeding butterfly species dominance and increases spatial turnover in floodplain forests of central Amazonia. *Ecology and Evolution*, *13*, Article e9718. https://doi.org/10.1002/ece3.9718

Pritt, J. J., & Frimpong, E. A. (2014). The effect of sampling intensity on patterns of rarity and community assessment metrics in stream fish samples. *Ecological Indicators*, *39*, 169–178. https://doi.org/10.1016/j.ecolind.2013.12.016

Richard, J. C., Castello, L., Gurdak, D. J., Peoples, B. K., & Angermeier, P. L. (2018). Size-structured habitat selection by arapaima in floodplain lakes of the lower Amazon. *Aquatic Conservation: Marine and*

*Freshwater Ecosystems*, *28*, 1403–1413. https://doi.org/10.1002/aqc.2969

Richardson, B. M., & Flinn, M. B. (2019). Increased probability and efficiency of gar capture using multi- vs. monofilament gill nets. *Journal of Fish and Wildlife Management*, *10*, 551–562. https://doi.org/10.3996/112018-JFWM-101

Rieucau, G., Boswell, K. M., Kimball, M. E., Diaz, G., & Allen, D. M. (2015). Tidal and diel variations in abundance and schooling behavior of estuarine fish within an intertidal salt marsh pool. *Hydrobiologia*, *753*, 149–162. https://doi.org/10.1007/s10750-015-2202-8

Roberts, H. C., Acre, M. R., Claus, M. P. A., Kappen, F. J., Winemiller, K. O., Daugherty, D. J., & Perkin, J. S. (2023). Tributary streams provide migratory fish with access to floodplain habitats in a regulated river: Evidence from Alligator Gar, *Atractosteus spatula*. *Canadian Journal of Fisheries and Aquatic Sciences*, *80*, 393–407. https://doi.org/10.1139/cjfas-2022-0076

Robertson, C. R., Zeug, S. C., & Winemiller, K. O. (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. https://doi.org/10.1111/j.1600-0633.2007.00265.x

Ruetz, C. R., Uzarski, D. G., Krueger, D. M., & Rutherford, E. S. (2007). Sampling a littoral fish assemblage: Comparison of small-mesh fyke netting and boat electrofishing. *North American Journal of Fisheries Management*, *27*, 825–831. https://doi.org/10.1577/M06-147.1

Scarnecchia, D. L. (1992). A reappraisal of gars and Bowfins in fishery management. *Fisheries*, *17*, 6–12. https://doi.org/10.1577/1548-8446(1992)017<0006:AROGAB>2.0.CO;2

Schlechte, J. W., & Buckmeier, D. L. (2021). Angler practices and preferences for managing Alligator Gar in Texas. *Journal of the Southeastern Association of Fish and Wildlife Agencies*, *8*, 23–31.

Schramm, H. L., & Ickes, B. S. (2016). The Mississippi River: A place for fish. In Y. Chen, D. Chapman, J. Jackson, D. Chen, Z. Li, K. Killgore, & Q. Phelps (Eds.), *Fishery resources, environment, and conservation in the Mississippi and Yangtze River basins* (pp. 3–34). American Fisheries Society. https://doi.org/10.47886/9781934874448.ch1

Schumann, D. A., Colvin, M. E., Miranda, L. E., & Jones-Farrand, D. T. (2020). Occurrence and co-occurrence patterns of gar in river–floodplain habitats: Methods to leverage species coexistence to benefit distributional models. *North American Journal of Fisheries Management*, *40*, 622–637. https://doi.org/10.1002/nafm.10402

Seidensticker, E. P. (1988). Comparison of gill nets and jug lines for selectively harvesting large gar. *Journal of the Southeastern Association of Fish and Wildlife Agencies*, *42*, 229–233.

Sendek, A., Kretz, L., van der Plas, F., Seele-Dilbat, C., Schulz-Zunkel, C., Vieweg, M., Bondar-Kunze, E., Weigelt, A., & Wirth, C. (2021). Topographical factors related to flooding frequency promote ecosystem multifunctionality of riparian floodplains. *Ecological Indicators*, *132*, Article 108312. https://doi.org/10.1016/j.ecolind.2021.108312

Sibley, E. C. P., Elsdon, T. S., Marnane, M. J., Madgett, A. S., Harvey, E. S., Cornulier, T., Driessen, D., & Fernandes, P. G. (2023). Sound sees more: A comparison of imaging sonars and optical cameras for estimating fish densities at artificial reefs. *Fisheries Research*, *264*, Article 106720. https://doi.org/10.1016/j.fishres.2023.106720

Smith, O. (2008). *Reproductive potential and life history of Spotted Gar* Lepisosteus oculatus *in the upper Barataria estuary, Louisiana* [Unpublished master's thesis]. Nicholls State University.

Smith, N. G., Buckmeier, D. L., Daugherty, D. J., Bennett, D. L., Sakaris, P. C., & Robertson, C. R. (2020). Hydrologic correlates of reproductive success in the Alligator Gar. *North American Journal of Fisheries Management*, *40*, 595–606. https://doi.org/10.1002/nafm.10442

Smith, N. G., Daugherty, D. J., Brinkman, E. L., Wegener, M. G., Kreiser, B. R., Ferrara, A. M., Kimmel, K. D., & David, S. R. (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. https://doi.org/10.1002/nafm.10369

Smylie, M., Shervette, V., & McDonough, C. (2015). Prey composition and ontogenetic shift in coastal populations of Longnose Gar *Lepisosteus osseus*. *Journal of Fish Biology*, *87*, 895–911. https://doi.org/10.1111/jfb.12759

Smylie, M., Shervette, V., & McDonough, C. (2016). Age, growth, and reproduction in two coastal populations of Longnose Gars. *Transactions of the American Fisheries Society*, *145*, 120–135. https://doi.org/10.1080/00028487.2015.1111256

Snedden, G. A., Kelso, W. E., & Rutherford, D. A. (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. https://doi.org/10.1577/1548-8659(1999)128<0144:DASPOS>2.0.CO;2

Snow, R. A., Stewart, D. R., Porta, M. J., & Long, J. M. (2020). Feeding ecology of age-0 gar at Texoma Reservoir inferred from analysis of stable isotopes. *North American Journal of Fisheries Management*, *40*, 638–650. https://doi.org/10.1002/nafm.10436

Speas, D. W., Walters, C. J., Ward, D. L., & Rogers, R. S. (2004). Effects of intraspecific density and environmental variables on electrofishing catchability of Brown and Rainbow trout in the Colorado River. *North American Journal of Fisheries Management*, *24*, 586–596. https://doi.org/10.1577/M02-193.1

Thomaz, S. M., Bini, L. M., & Bozelli, R. L. (2007). Floods increase similarity among aquatic habitats in river–floodplain systems. *Hydrobiologia*, *579*, 1–13. https://doi.org/10.1007/s10750-006-0285-y

Valentine, J. M., Walther, J. R., McCartney, K. M., & Ivy, L. M. (1972). Alligator diets on the Sabine National Wildlife Refuge, Louisiana. *The Journal of Wildlife Management*, *36*, 809–815. https://doi.org/10.2307/3799434

Velez, S. (2015). Effects of ultrasonic frequencies on schooling behavior of American Shad (*Alosa sapidissima*). *Journal of Aquaculture & Marine Biology*, *2*, Article 00019. https://doi.org/10.15406/jamb.2015.02.00019

Wegener, M. G., Harriger, K. M., Knight, J. R., & Barrett, M. A. (2017). Movement and habitat use of Alligator Gars in the Escambia River, Florida. *North American Journal of Fisheries Management*, *37*, 1028–1038. https://doi.org/10.1080/02755947.2017.1342722

Wei, Y., Duan, Y., & An, D. (2022). Monitoring fish using imaging sonar: Capacity, challenges and future perspective. *Fish and Fisheries*, *23*, 1347–1370. https://doi.org/10.1111/faf.12693