ORIGINAL ARTICLE

Mississippi River-floodplain connectivity level mediates fish assemblage dynamics

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ABSTRACT

The life histories of many Louisiana fishes are tied to the timing, magnitude, and duration of the Mississippi River flood pulse. Anthropogenic modifications designed to control and restrict flood waters have decoupled Louisiana's floodplains from the seasonal flood pulse, influencing the aquatic food web. Culvert and rock weir repair within the Richard K. Yancey Wildlife Management Area aims to improve water quality and maintain appropriate water depth for native Louisiana fishes. In this study we conducted high-resolution imaging sonar (ARIS Explorer 3000) monitoring of the floodplain fish assemblage across seasons prior to hydrologic restoration. Imaging sonars may be used to obtain quantitative ecological and behavioral information without the selectivity biases of traditional techniques through the recording of continuous video-like datasets that are not constrained by environmental factors such as turbidity. Our first objective was to test the hypothesis that seasonal inundation levels and proximity to the Mississippi River affect the abundance and size class distribution of the floodplain-associated fish assemblage. Our second objective was to characterize species composition and ecological function of each acoustically-detected size class using historical fisheries datasets collected by the Louisiana Department of Wildlife and Fisheries. To do so, we employed the multi-gear mean standardization technique for standardizing catch per unit effort of passive and active gear types used within the historical dataset in order to produce a non-exhaustive list of potentially recorded species by the imaging sonar. Our study demonstrated a size class dependent use of floodplain habitats mediated by inundation level, but not the distance from the Mississippi River. Our results illustrated a trend of increased detections of all size classes during high-water connected-spring and summer periods, as well as during disconnected-summer periods immediately following the seasonal flood pulse. Continued monitoring of the fish assemblage will provide additional data to better describe the complex dynamic patterns the floodplain fish assemblage may exhibit in response to the seasonal flood pulse and hydrologic restoration efforts.

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INTRODUCTION

Large river-floodplains consist of interconnected lowland habitats characterized by varying inundation levels due to lateral overflow from the main-stem river during seasonal flood pulses (Junk, 1989). Flood pulses within unaltered systems mediate complex abiotic and biotic interactions (Junk, 1989; Petsch *et al*., 2023), hydrologically linking floodplain habitats and facilitating the mixing of resources from aquatic and terrestrial systems. This connectivity supports high levels of productivity (Molinari *et al*., 2021; De Gallardo *et al*., 2023). Hydrological connectivity also influences various aspects such as water quality, fish species abundance, diversity, distribution, and trophic interactions (Mitsch *et al*., 2008; Cazzanelli *et al*., 2021; Munyai *et al*., 2023).

Fish assemblages in floodplain systems often shift in response to environmental changes (Arthington and Balcombe 2011; Burgess *et al*., 2012; Rantala *et al*., 2016) associated with the seasonal flood pulse. Rising flood waters prompt many fishes to leave habitats in or near the main-stem channel (Arantes and Cetra 2011; Castello *et al*., 2019) and seek areas of flooded vegetation to forage, spawn, or hide from predators (Mosepele *et al*., 2022; Petsch *et al*., 2023). Receding floodwaters often serve as a cue to return to habitats closer to the mainstem channel (Arantes and Cetra, 2011; Buckmeiere *et al*., 2013; Castello *et al*., 2019; Ogaz *et al*., 2022), with those remaining in the isolated water bodies persisting between inundation periods (Magoulick and Kobza *et al*., 2003; Wang *et al*., 2019). The ecological explanations (*i.e.*, functions) underlying the fish assemblage use of the different floodplain habitats is highly complex as it varies not only between species, but also between ontogenetic levels, across fluctuating patterns of inundation (Rypel *et al*.,. 2012; Bolland *et al*., 2015; Richard *et al*., 2018).

The floodplain of the Lower Mississippi River Basin (LMRB) has been heavily altered by anthropogenic modifications to control flooding (Eggleton *et al*., 2016). Originally spanning 10.1 million ha, the LMRB has been reduced to less than 8% of its original size (Schramm and Ickes, 2016). Construction of levees and water control structures within and beyond the state of Louisiana has disconnected floodplain habitats so that inundation in many areas only occurs during high precipitation events (Nelson *et al*., 2002). This irregular pattern of inundation may impact fishes adapted to the typical hydrology pattern of the LMRB (King *et al*., 2009; Alford and Walker, 2013), which is high water in the spring and low water in the fall (Kemp *et al*., 2014; Eggleton *et al*., 2016; Luo and Criss, 2018). Previous studies have identified differences in assemblage composition (Bennett and Kozak, 2016), diet (Bonvillain and Fontenot, 2020; Rixner *et al*., 2021) and habitat use (Bouloy *et al*., 2024) between areas of the LMRB which receive a reduced but consistent seasonal flood pulse and areas that are decoupled due to anthropogenic modifications. Planned hydrologic restoration efforts aim to enhance fish passage and improve water retention in order to mitigate the impacts of a decoupled flood pulse. As such, continued monitoring of fish assemblages in the LMRB is essential to establish baselines, assess the effectiveness of these restoration activities, and to guide future management strategies.

The use of traditional gear types such as electrofishing or gill-nets may lead to biased results through inherent species-specific gear vulnerability, size-selectivity of the gear type or through the disturbance and removal of the individual(s). Increasing spatial and temporal scales of an assemblage survey typically requires multiple gear types with repeated efforts to achieve a more accurate assessment of assemblage structure (Bayley and Austen, 2002; Kennard *et al*., 2006; Price and Peterson, 2010). Repeated efforts in the short-term, such as multiple passes when electrofishing, may influence detection probability as the assemblage responds to the disturbances (Peterson *et al*., 2004; Pritt *et al*., 2014; Pritt and Frimprong, 2014). Inferences about behavior at the level of the individual *(i.e.* fine-scale) are diminished (Ngyuen *et al.*, 2023) through the removal of individuals from the population, negating social or competitive interactions Moreover, collected individuals may not represent the behavior of the assemblage due to differences in behavior between males and females of a species which may affect capture probability (Šmejkal *et al*., 2022). Environmental DNA (eDNA) is an alternative non-invasive approach that is increasingly used within aquatic environments to identify species presence without requiring direct capture (Roussel *et al*., 2015; Hanfling *et al*., 2016; Evans *et al*., 2017). While eDNA may provide some taxonomic resolution, it does not offer information about assemblage dynamics such as abundance, behavior, movement, or size structure. Therefore, while traditional gear types and molecular approaches have distinct advantages, the limitations of each necessitate complementary methodologies to further the assessment of fish assemblages.

Innovations in advanced observational sampling technologies, such as imaging sonars, offer a means to study aquatic ecosystems at the level of individual organisms through video-like data recorded in situ. Operating at high frequencies (0.7-3 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 selectivity biases of traditional techniques and are not limited by environmental factors like turbidity (Speas *et al*., 2004; Lyon *et al*., 2014; Munnelly *et al*., 2024). Recent research has established the ability of this technology to non-intrusively monitor complex habitats and resolve behavioral research gaps in highly turbid or low-visibility environments (Wei *et al*., 2022; Sibley *et al*., 2023; Munnelly *et al*., 2024). In the LMRB, where high turbidity precludes the use of traditional underwater cameras, imaging sonars provide a viable alternative for studying aquatic fauna in their natural environment. Despite the now well-demonstrated performance of imaging sonar for studying behavioral interactions in fish and its effectiveness in complex habitats independent of light intensity or turbidity, this technology is not without limitations. Species identification remain a challenge inherent to imaging sonars (Munnelly *et al*., 2024). 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 the video-like datasets.

In this study we hypothesized that the degree of river-floodplain connectivity influences the relative abundance and size-class distribution of the associated fish assemblage, with higher levels of connectivity supporting a greater relative abundance and larger size classes. To test this hypothesis, our primary objective was to quantify these patterns while accounting for seasonal variation. We used advanced high-resolution imaging sonar (Adaptive Resolution Imaging Sonar "ARIS" Explorer 3000, Sound Metrics Corporation, Bellevue, Washington, USA) to monitor the floodplain fish assemblage during periods of high water (connected) and low water (disconnected) across all four seasons (spring, summer, fall, winter) at four distinct 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 Wildlife Management Area, providing a critical baseline for future comparisons of fish abundance and size-class distribution in response to these efforts.

The secondary objective of our study was to characterize the species composition and ecological function of each acoustically-detected size class. To achieve this objective while mitigating the challenge of species-level identification in imaging sonar footage, five size-classes were created to capture generalized functional groups (*i.e.*, small prey, small predator, large predator) to aid in assessment of ecological function and relevance (*i.e.*, foraging, reproduction) of floodplain habitat use. Grouping fauna into generalized functional-guilds (Welcomme *et al*., 2006) can be an effective method to monitor spatiotemporal variability in fish assemblage structure. Often these guilds encompass generalized life-histories, reproductive patterns, or trophic levels (Wang *et al*., 2019; Oliveira *et al*., 2020). Although grouping species into guilds may discard or obscure species-specific differences when unknown, guilds typically retain enough information to simplify complex communities into manageable and ecologically meaningful units (Benoit *et al*., 2021; Fournier *et al*., 2021). In addition, we used historic Louisiana Department of Wildlife and Fisheries (LDWF) fish assemblage datasets to help ascertain the species composition of each size-class and the potential ecological functions served by the floodplain.

METHODS

Study site

We conducted imaging sonar monitoring of the fish assemblage at the Richard K. Yancey Wildlife Management Area (WMA) near Vidalia, Louisiana, between 7 August 2021 and 10 January 2023. Located on the western bank of the Mississippi River, the WMA (31.18896, -91.63190) consists of 28,328 ha of floodplain habitat (Fig. 1). Inundation of the WMA begins at a rock weir located in the southern portion of the WMA, immediately adjacent to the Mississippi River, before entering

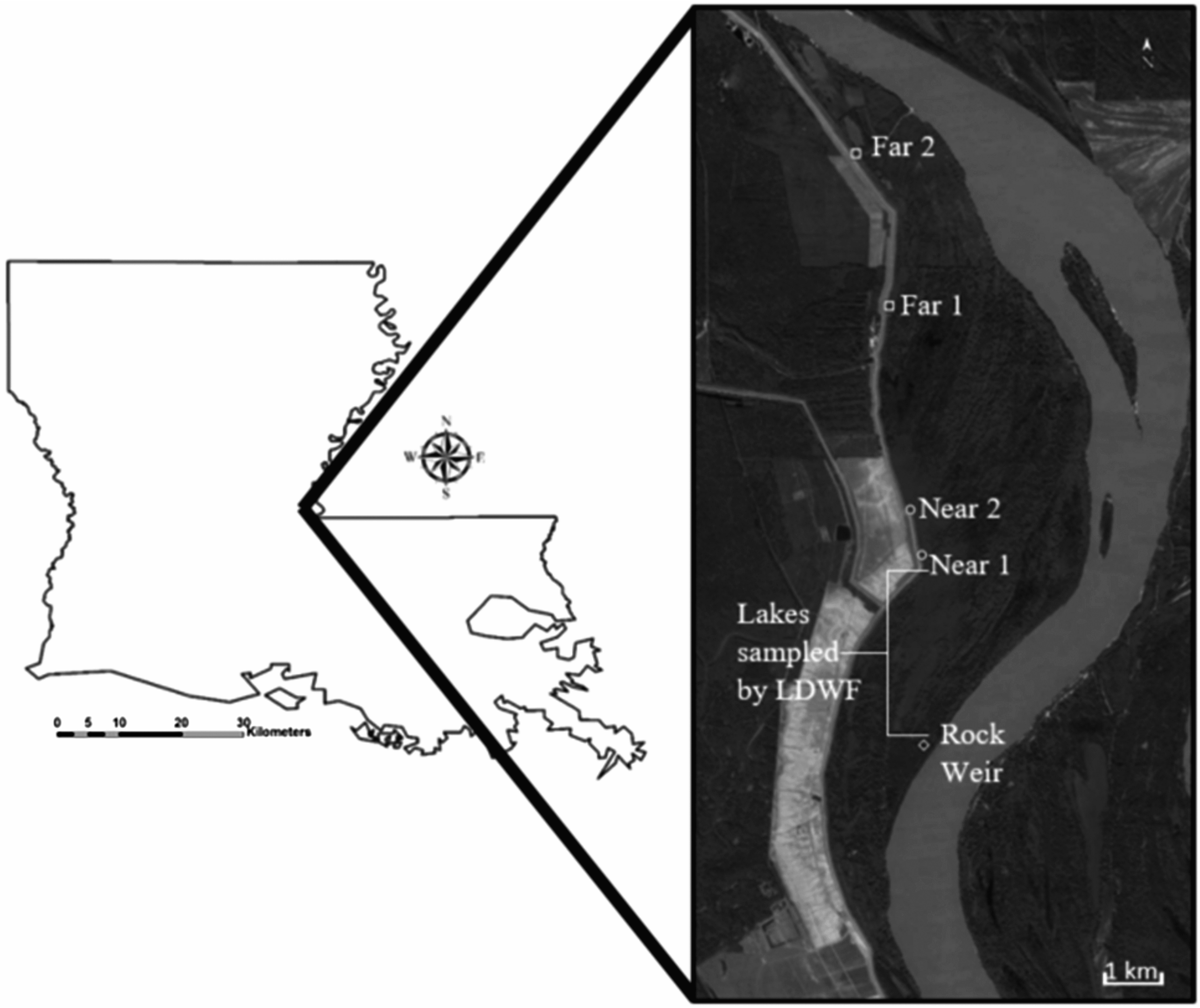

Fig. 1. Richard K. Yancey Wildlife Management Area within map in-set. Circles represent near sites; squares represent far sites. Diamond represents the rock weir; the initial inundation point for the WMA.

three floodplain lakes. These lakes are inundated year-round but are disconnected from the main-stem river during low water. Rising flood waters eventually connect these lakes to the northern portions of the WMA through a series of culverts and bayous (Fig. 1). Surveys were conducted in 238 ha of the WMA that will undergo hydrologic restoration via culvert and rock weir repair/replacement to improve water quality and facilitate fish passage (Fig. 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 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 flood waters from entering elsewhere.

Four sites (n=4) that experience a moving littoral edge (*i.e.*, aquatic-terrestrial transition zone; Junk *et al.*, 1989) were haphazardly chosen as representative floodplain habitats along a south to north gradient (Fig. 1). These four sites were qualitatively classified according to respective relative distances (near or far) to the rock weir. Near sites (approximately 2.75 and 3.0 km straight-line distance to rock weir, respectively) consistently received more frequent inundation via the flood pulse, beginning in early spring. In contrast, far sites (approximately 6.2 and 8.6 km straight-line distance to rock weir, respectively) required higher river stages to become connected to the main-stem compared to near sites, which occurred in mid to late spring (Fig. 2). Natural and anthropogenic barriers within the WMA, in addition to subtle elevation changes, hindered complete inundation of the WMA until river stage reached appropriate levels (Fig. 2). The low elevation at all four sites facilitated consistent inundation of the isolated water bodies between flood events. We used qualitative designations to categorize the inundation levels witnessed in the WMA. “Connected” was defined as all four sites being simultaneously inundated by Mississippi River flood waters. “Disconnected” referred to when all four sites were hydrologically separated from the Mississippi River and from each other. Categorical inundation levels were determined by Knox River Landing gauge measurements (https://waterdata.usgs.gov/monitoring-location/07294800/#parameterCode=00065&period=P7D) and from visual observations at the sites. The 13 sampling days were first categorized by floodplain inundation level, then by season: Connected-spring (2 March 2022, 9 April 2022, 29 April 2022, 27 May 2022), connected-summer (16 June 2022), disconnected-summer (7 August 2021, 22 July 2022, 30 July 2022), disconnected-fall (30 October 2021, 15 September 2022, 30 October 2022) and disconnected-winter (18 December 2022, 10 January 2023). Only one connected-summer day could be sampled (16 June 2022) due to rapid dewatering of the floodplain. The 22 July 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.

Data collection

A high-resolution imaging sonar (ARIS 3000 - Adaptive Resolution Imaging Sonar, Sound Metrics Corp.; Fig. 3), operating at 3 MHz, was secured to a weighted polyethylene platform (33 cm x 33 cm x 28 cm), and manually deployed from a stationary position approximately 1 m from the bank, resting on the bottom of the floodplain. The sonar was positioned perpendicular to the water column to minimize interference from the

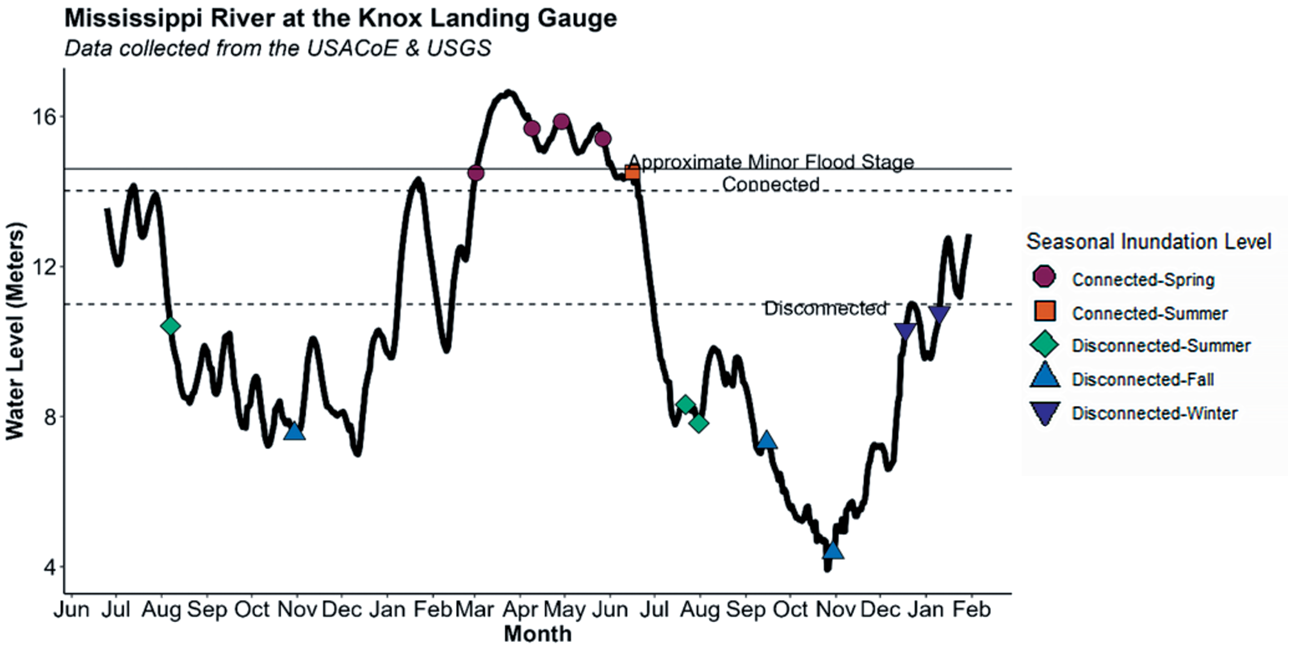

Fig. 2. Hydrograph representing the timeline of sampling; 7 August 2021 to 20 January 2023. Approximate levels of inundation experienced within the WMA are represented by dashed lines. Partial inundation, an inundation level in which only near sites would be connected by flood waters, is represented as the space between dashed lines and was only sampled by the Louisiana Department of Wildlife and Fisheries. Minor flood stage of the Mississippi River represented by the solid line.

surface or bottom of the floodplain. Sites were greater than the 20 m maximum range of the ARIS and were unable to be monitored from shore to shore, therefore, a range of 8 m was selected to increase resolution and improve the accuracy of fish detections. Recording at approximately 10 frames per s, the ARIS sonar consistently sampled a three-dimensional volume of water within a 30° x 14° field of view at the selected range of 8 m. Maximum water depth within the field of view did not typically exceed 3 m, however, water depths outside the field of view could surpass 3 m, particularly during the flood pulse. 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 that excluded the area behind the sonar that faced the bank. Sampling at each of the four sites occurred on each sample date between sunrise (approximately 06:30) and sunset (approximately 17:30), with the exception of 22 July 2022 when only two sites were sampled due to equipment failure. Site order was randomly determined for each sampling prior to ARIS deployment. A 5-min acclimatization period was implemented to allow aquatic fauna to resume normal behaviors following the minor disturbance caused by the manual deployment of the imaging sonar near the shoreline.

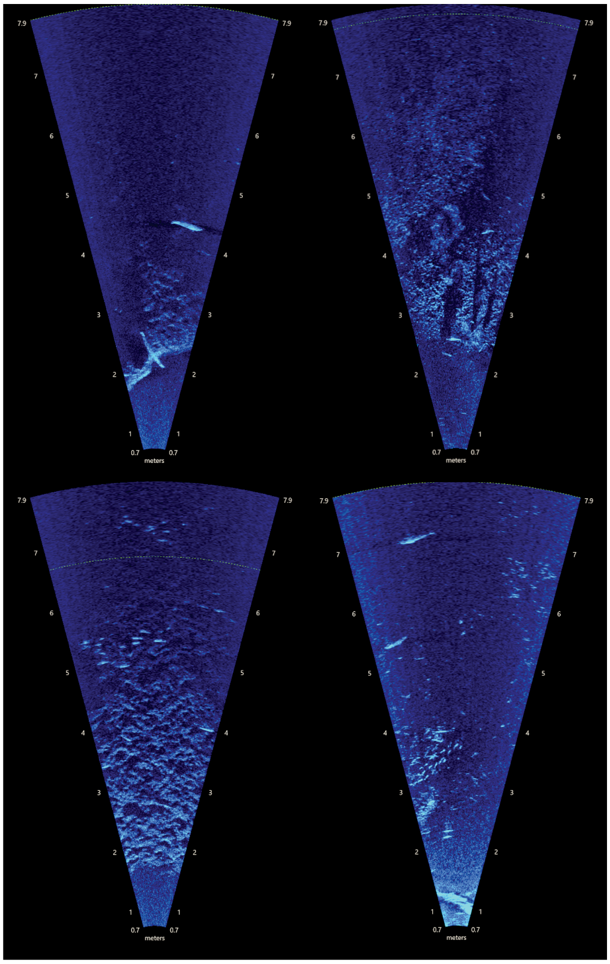

Fig. 3. Examples of the high-resolution video data, presented as screenshots, from the ARIS Explorer 3000.

Quantification of fish abundance and size-class distribution

Relative fish abundance was estimated using the MaxN method (Cappo *et al*., 2004) and is defined as the maximum number of individuals recorded within the field of view. Prior research has used the MaxN method to estimate relative fish abundance from data collected *via* high-resolution imaging sonars (Becker *et al*., 2011; Rieucau *et al*., 2015). In order to include the maximum number of fish observed we manually reviewed all the frames (approximately 2,000,000 frames) within the ARIS recordings. Individual fish leaving the FOV and later coming back were counted as new individuals. Total body length (mm) of each individual fish was manually measured using the ArisFish software (Sound Metrics Corporation, Bellevue, Washington, USA). To minimize errors in obtaining total body length estimate via sonar (Becker *et al.* 2011), measurements were taken when the individual was orientated approximately perpendicular to the sonar lens, beginning from the head. While this approach is labor intensive, it ensured precision in fish counts and size measurements.

Identification of species remains a challenge for imaging sonar datasets (Munelley *et al*., 2023), therefore we describe potential ecological function and relevance of floodplain habitat use for fishes in the following size-classes: I: 200-400 mm, II: 400-600 mm, III: 600-800 mm, IV: 800-1000 mm, and V: greater than 1000 mm. Fish below 200 mm were present in the dataset, but given their exceptionally high abundance, were excluded from further analysis. Therefore, we focus on larger individuals that are likely to have different ecological roles and patterns of habitat use. The number of size classes is different from the number of life stages because of size variation across species.

Describing the fish assemblage using historical datasets

Using datasets collected by the Louisiana Department of Wildlife and Fisheries (LDWF), we compiled a non-exhaustive list (*Supplementary Tab. S1*) of floodplain-associated fishes that may be detected through imaging sonar monitoring. High turbidity within LMRB floodplain habitats precludes the use of traditional underwater cameras for use in species identification, making historical datasets an essential resource for characterizing species composition and ecological function. Spanning 2018 to 2023, LDWF sampling efforts occurred in the three lakes situated in the southern portion of the WMA employing active and passive gear types; electrofishing, mono-filament gill nets, frame nets, and seining. To facilitate comparisons between the four traditional gear types and the imaging sonar, we employed the multi-gear mean standardization (MGMS) technique outlined by Gibson-Reinemer *et al*. (2016) for standardizing catch per unit effort (CPUE) data. Calculating MGMS begins by standardizing the CPUE data for each gear type using a form of mean centering. Units of effort for each gear type are canceled out during calculation while preserving patterns of relative abundance within and across observations. For each species the standardized data from each gear type was then summed to provide an estimate of the possible taxonomic composition of the fish assemblage detected by the imaging sonar (*Supplementary Tab. S1*). We use FishBase (www.fishbase.org) and associated references to further inform our explanations of possible species composition and potential ecological functions for each of the five size classes.

Statistical analyses

Observations (*i.e.*, counts) of fish in each size class were recorded for each site (near 1, near 2, far 1, far 2) and the corresponding seasonal inundation level (*i.e.*, connected-spring, disconnected-summer, *etc*.). Means and standard errors were calculated for each seasonal inundation level and site location, maintaining the independence of each specific site to ensure greater precision than if sites were pooled. Prior to univariate and multivariate analyses, fish detections (*i.e.*, counts) *via* imaging sonar monitoring were also standardized using MGMS to facilitate comparisons with the LDWF dataset (Gibson-Reinemer *et al*., 2016). A Pearson's Chi-Squared test was used to examine if detections via imaging sonar monitoring, regardless of size class, 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 fish detections at near and far sites did not vary between 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. First, non-metric multidimensional scaling (NMDS) with the Bray-Curtis dissimilarity matrix was used to visualize dissimilarities in a reduced dimensional space using the metaMDS function of the vegan package in R (The 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 samples, (*i.e.*, combinations of date, site, and proximity to the Mississippi River) based on the seasonal inundation level (*i.e.*, connected-spring, disconnected-summer). Patterns were further analyzed using permutational MANOVA (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 from the Mississippi River, or their interaction. Permutational pairwise comparisons (*p*-values adjusted for multiple comparisons using the False Discovery Rate, FDR) were conducted using the RVAideMemoire package in R with 10,000 permutations. All analyses were performed using R. 4.2.2.

RESULTS

We collected 56 h of ARIS footage from 7 August 2021 to 10 January 2023 resulting in 9,546 fish detections across all five size-classes (Tab. 1). Size class I accounted for 89.2% (n=8,496) of the total fish detections within our study (Tab. 1). Connected-spring periods accounted for approximately 41.3% (n=3,510) of the total detections for size class I wherein the mean number of detections was 2,115 (264.38±188.68) at the far sites and 1,395 (155.00±98.55) at the near sites. Fish in size class II (n=832) and size class III (n=182) accounted for 8.7% and 1.9% of the total dataset, respectively (Tab. 1). Fish in the two largest size-classes (IV and V) accounted for less than 1% of the dataset (0.25% and 0.08%, respectively; Tab. 1).

A non-significant association between the seasonal inundation level and the proximity to the Mississippi River was revealed by the chi-square test ($X^2=0.67$, df=4, $p=0.96$), suggesting that at the assemblage level no differences in fish detections were observed between the floodplain connectivity variables of seasonal inundation level and proximity to inundation source (Fig. 4). The NMDS revealed notable monotonic relationships between the size-classes used with the study and the NMDS dimensions (Fig. 5). Samples were widely spread out over the first MDS axis, but tended to cluster around the center of the second MDS axis. Overall, the fish assemblage structure differed ($R=0.25$; $p<0.001$), with seasonal inundation level in the WMA being the only significant factor (Tab. 2, Fig. 5). Dissimilar distributions (FDR adjusted) were recorded between connected-spring and disconnected-summer ($p=0.041$), connected-spring and disconnected-fall ($p=0.024$), disconnected-summer and disconnected-fall ($p=0.007$), and disconnected-summer and disconnected-winter ($p=0.007$) (Tab. 3). While dissimilar distributions were also recorded between connected-summer and disconnected-fall ($p=0.012$), and between connected-summer and disconnected-winter ($p=0.024$), caution should be exercised when interpreting these results as only one connected-summer event could be sampled.

DISCUSSION

Our study demonstrates the use of floodplain habitats by the associated fish assemblage was partially affected by the degree of Mississippi River floodplain connectivity. We found that relative abundance of fish assemblage, regardless of size class, did not differ between seasonal inundation levels and proximity to the point of inundation by the Mississippi River. Contrary to the abundance results, distribution of size classes does appear to be influenced by the seasonal inundation level. Dissimilar distributions detected were recorded between connected-spring and disconnected-summer, connected-spring and disconnected-fall, disconnected-summer and disconnected-fall, as well as disconnected-summer and disconnected-winter. Our results illustrate a trend of increased detections of all size classes during high-water connected periods and during disconnected-summer periods immediately following the seasonal flood pulse. Interestingly, the differences between connected-spring and disconnected-summer may be explained in part by decreased detections of size class I and V, and an increase in detections of size classes II, III, and IV. Differences between connected-spring and disconnected-fall, disconnected-summer and disconnected-fall, as well as disconnected-summer and disconnected-winter indicate a decreasing pattern in detections of each size class as the floodplain remains disconnected.

Using LDWF data (following CPUE standardization), the possible taxonomic composition of each size class was informed from the most common species to occur in each seasonal inundation level. Given that the high turbidity of LMRB floodplain habitats precludes the use of traditional underwater cameras for species identification, this approach provided a practical means of interpreting imaging sonar detections. It is important to note that this is not meant to produce a definitive list of species detected *via* imaging sonar monitoring, but instead represents an attempt to characterize the species composition and ecological function of each acoustically-detected size class. Species below our established minimum size threshold of 200 mm are excluded from discussion. These include *C. venusta, F. chrysotus, Gambusia* spp., *L. humilis, L. sicculus, M. audens,* and *P. caprodes*.

Size class I, accounting for 89.2% of all fish detected via imaging sonar, includes individuals across different age classes, varying by species and functional response. Within this size class, fish face predation pressures from multiple sources including American Alligators (*Alligator mississippiensis*), piscivorous birds, mammals, and larger fish predators (Valentine, 1972; Delong, 2010; Snow *et al*., 2020). The three most abundant species from the LDWF datset, following CPUE standardization, were *D. petenense*, *P. nigromaculatus,* and *D. cepedianum*, all of which are prey species in floodplain systems like the LMRB (Miller *et al*., 2015; Burdis *et al*., 2020; Smith *et al*., 2020). These species show higher abundance during connected-spring or connected-summer periods with somewhat lesser prevalence during disconnected-summer periods, consistent with imaging sonar observations of size class I. Seemingly less abundant species that may serve similar ecological roles include; *L.*

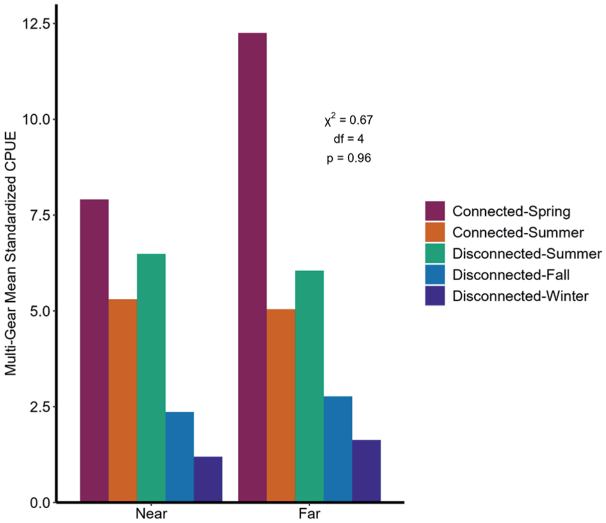

Fig. 4. Bar plot depicting the results of the chi-square analysis comparing the seasonal level of inundation (*i.e.*, connected-spring, disconnected-summer) and proximity to the Mississippi River (near or far). Prior to analysis, fish detections (*i.e.*, counts) via imaging sonar monitoring were standardized, regardless of size class, using multi-gear mean standardization (MGMS).

Table 1. MaxN of fish (n), by size class, with respect to seasonal inundation level and proximity to the Mississippi River, with the mean ±SE number of fish within those ob±servations. Means and standard errors were calculated on unpooled sites, maintaining distinctions based on site location (*i.e.*, near 1/far 1) and seasonal inundation level *(i.e.*, connected-spring).

	Proximity to Mississippi River			
	Near		Far	
Size class (mm)	**n**	**Avg. n fish±SE**	**n**	**Avg. n fish±SE**
Connected spring				
I	1395	155.00±98.55	2115	264.38±188.68
II	62	6.89±1.84	154	19.25±7.01
III	20	2.22±1.15	13	1.63±0.56
IV	2	0.22±0.22	5	0.63±0.26
V	1	0.11 ±0.11	5	0.63±0.42
Connected summer				
I	950	475.00±393.00	920	460.00±335.00
II	36	18.00±3.00	21	10.50±6.50
III	5	2.50±2.50	3	1.50±1.50
IV	1	0.50±0.50	0	0
V	0	0	0	0
Disconnected summer				
I	876	175.20±72.03	1039	207.80±49.36
II	248	49.60±23.31	77	15.40±3.37
III	75	15.00±6.38	14	2.80±0.58
IV	13	2.60±1.08	0	0
V	1	0.20±0.20	1	0.20±0.20
Disconnected fall				
I	316	52.67±6.76	434	72.33±22.32
II	94	15.67±4.40	71	11.83±2.92
III	31	5.17±1.96	11	1.83±0.91
IV	1	0.17±0.17	2	0.33±0.21
V	0	0	0	0
Disconnected winter				
I	182	45.50±14.92	269	67.25±17.21
II	38	9.35±6.74	31	7.75±3.82
III	4	1.00±0.71	6	1.50±0.87
IV	0	0	0	0
V	0	0	0	0

macrochirus, *C. carpio*, *L. megalotis*, *P. annualris*, *L. gulosus*, and *L. microlophus*. Additionally, smaller bodied Largemouth Bass (*M. nigricans*), buffalo (*I. bubalus*, *I. niger, I. cyprinellus*), catfish (*I. punctatus, P. olivaris*, *I. furcatus*), Striped Mullet (*M. cephalus*), Gar (*A. spatula, L. oculatus, L. osseus, L. platostomus*), and Emerald Bowfin (*A. ocellicauda*) may have been observed through imaging sonar monitoring as either young-of-the-year (YOY), juveniles, or sub-adults. Flood pulses that occur during the spawning season impact the reproductive success and recruitment of these species (Clark *et al*., 2008; Alford and Walker, 2013). For example, recruitment of *M. nigricans* to age-1 and age-2 is positively correlated to flood duration and magnitude from the previous years (Alford and Walker, 2013). Young-of-the-year and juveniles of these species continue to use the flooded areas as refugia and nursery habitats (Alford and Walker, 2013; Seibert *et al*., 2017; Radigan and Fincel, 2019; Cruz *et al*., 2020; McAllister *et al*., 2023; Leblanc and Farrell, 2023; Bouloy *et al*., 2024; Williams *et al*., 2024).

Less than 10% of the total observations from imaging sonar monitoring were accounted for by size class II and III. Both size classes exhibit a more pronounced, albeit more variable, association with disconnected periods in the summer and fall. In contrast, while their abundance was lower, detection of both size classes during connected-spring periods seems to exhibit less variability. Large individuals of *P. nigromaculatus* and *D. cepedianum* could compose a portion of these observations. More than likely, detections of these size classes are likely reproductively active adult *L. oculatus*, *I. bubalus*, *M. nigricans*, *I. punc-*

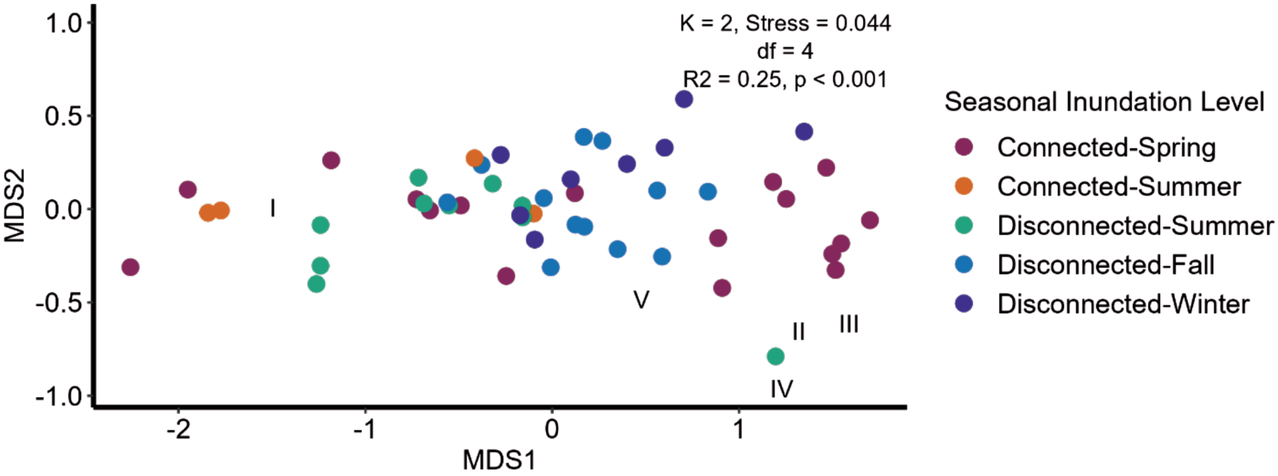

Fig. 5. Non-metric multidimensional scaling ordination (k=2, stress=0.044) of fish size-class distribution. Circles represent individual sampling events grouped by the seasonal inundation level, as tested within the PERMANOVA ($R^2 = 0.25$, $p<0.001$). Prior to multivariate analyses, fish detections (*i.e.*, counts) *via* imaging sonar monitoring were standardized, for each size class, using multi-gear mean standardization (MGMS). Data used were counts for each size-class from recorded ARIS footage of the WMA, untransformed, using a Bray-Curtis dissimilarity matrix and 10,000 permutations.

Table 2. Results of the PERMANOVA using seasonal level of inundation as the single explanatory variable following model parsimony. Prior to analysis, fish detections per size class *via* imaging sonar monitoring were standardized using the MGMS method. Analysis performed using the Bray-Curtis dissimilarity matrix.

	Df	SOS	R^2	F	Pr(>F)
Inundation	4	2.37	0.25	3.77	< 0.001
Residual	46	7.24	0.75	—	—
Total	50	9.61	1.00	—	—

Table 3. Summary of pairwise comparisons between seasonal inundation levels following permutation MANOVAs (PerMANOVA) on a Bray-Curtis distance matrix, fdr adjusted for multiple comparisons.

	Connected-spring	Connected-summer	Disconnected-summer	Disconnected-fall
Connected-summer	0.110	—	—	—
Disconnected-summer	0.041	0.430	—	—
Disconnected-fall	0.024	0.012	0.007	—
Disconnected-winter	0.099	0.024	0.007	0.452

tatus, *L. platostomus*, *I. niger*, *A. grunniens*, *L. osseus, I. cyprinellus,* and juvenile *A. spatula*. There are several plausible explanations for the tendency to observe these size classes during disconnected periods, specifically disconnected-summer. Resident species such as these will use floodplain habitats year-round to fulfill life history requirements (Buckmeier *et al*., 2013; Schramm and Ickes, 2016; Lackmann *et al*., 2023; Zolderdo *et al*., 2024). Notable exceptions include *L. osseus* and *A. spatula* that leave interior floodplain habitats and inhabit areas closer to the main-stem channel during low water periods (McGrath, 2010; Smith *et al*., 2020). Alternatively, as flood-waters recede, formerly inundated habitats become inaccessible and the relative abundance of these size classes increases per inundated area. The rate with which flood waters receded during disconnected-summer periods may also have isolated certain species from the floodplain lakes. Given that the plausible taxonomic composition of these size classes reflects resident species, we anticipate individuals in these size classes use the floodplain for foraging and spawning opportunities (Dattilo *et al*., 2021; Leblanc and Farrell, 2023).

The two largest size-classes, IV and V, accounted for less than 1% (n=32) of the imaging sonar dataset. Individuals in these size-classes would be expected to use the floodplain for foraging and reproductive opportunities (McGrath, 2010; Kluender *et al*., 2017; Wegener *et al*., 2017). Body shape and swimming style aided in the identification of 21 of the 32 fish observed in the two largest size-classes as one of the four species of gar. Adult *L. osseus* and juvenile *A. spatula* would be expected, with fewer adult *L. occulatus* and *L. plattostomus*, especially in the largest size-class (Ferrara, 2001; McGrath, 2010; Felterman, 2015; Smylie *et al*., 2015). Of the 21 fish identified as gar in these size classes, 17 were considered to be *L. osseus* by a narrow, elongated snout, with the remainder considered as *A. spatula* given the stout body and thicker snout. Both *A. spatula* and *L. osseus* were more frequently detected during disconnected periods in the floodplain lakes and at near sites. Dewatering of the floodplain has been associated with the emigration of *A. spatula* and *L. osseus* towards deep-water habitats nearer the main-stem (Buckmeier *et al*., 2013; Kluender *et al*., 2017). Due to the rapid dewatering of the floodplain during summer 2022, a plausible explanation as to why *A. spatula* and *L. osseus* were detected at near sites during low water periods was that individuals were unable to leave the interior floodplain before flood waters receded below natural and anthropogenic barriers. The remaining 11 individuals observed in the two largest size-classes could be the following species which regularly inhabit large river-floodplain systems; *I. bubalus*, *I. punctatus*, *C. carpio, I. niger*, *P. olivaris*, *I. cyprinellus*, *M. piceus*, *I. furcatus*, *H. nobilis*, and *C. idella* (Miranda and Killgore, 2019; Lackmann *et al*., 2023). The carangiform locomotion exhibited by these individuals would suggest either buffalo or introduced carps, with standardized CPUE suggesting *I. bubalus* as the most likely species, followed by *C. carpio,* and *I. niger*. All three potential species were more abundant during disconnected periods in the LDWF dataset, specifically disconnected-summer, and may explain some of the individual detected via imaging sonar monitoring.

Our findings suggest that floodplain habitat use is influenced, at least in part, by seasonal floodplain connectivity. The proposed ecological functions of floodplain habitat use associated with each size class may differ year-to-year given the variation in timing, magnitude, and duration of the flood pulse annually, emphasizing the need for additional monitoring. Planned restoration efforts in this area that are designed to improve fish passage and hydrology begets further work as these improvements may lead to measurable effects on the fish assemblage. For instance, size class I are likely to benefit from the increased availability of nursery and refuge habitats in order to alleviate predation pressures (Bolland *et al*., 2015; Williams *et al*., 2024), particularly during low water disconnected periods. Improving fish passage from the main channel to the interior floodplain, as well as between interior floodplain habitats, may facilitate access to and from foraging and spawning grounds for size classes II, III, IV, and V. Furthermore, these proposed changes may alleviate intra- and interspecific competition as all species may be able to acquire at least some of the available resources (Whitledge *et al*., 2022; Van Der Sleen and Rams, 2023). As restoration progresses, future imaging sonar work should focus on how increased connectivity and improved hydrology impacts the associated fish assemblage, particularly at the culverts. We also acknowledge the continued use of traditional gear types to "ground-truth" imaging sonar datasets in order to alleviate the challenge of species identification inherent to the technology. To this end, previously challenging questions such as monitoring predator-prey interactions, foraging behaviors, and reproductive-related activity may now be pursued in *situ*. The increasing availability of imaging sonars will, along with our study, contribute to the refinement of management actions and conservation strategies.

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Online supplementary material:

Tab. S1. Summary of species collected by the Louisiana Department of Wildlife and Fisheries.