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The Annual Flood Pulse Mediates Crayfish as a Major Diet Constituent of Carnivorous Fishes in South Louisiana

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ABSTRACT

Anthropogenic modifications to river-floodplain systems can decouple floodplains from mainstem inputs, alter flood pulse dynamics, and disrupt population dynamics and trophic web stability of aquatic biota. The Atchafalaya River Basin (ARB) receives an annual flood pulse from the Mississippi River that contributes to high crayfish abundance. Conversely, reduced crayfish abundance in the Barataria Basin (BB) is attributed to the system no longer receiving an annual flood pulse from the Mississippi River. Therefore, the purpose of this research was to determine if the absence of an annual flood pulse and reduced crayfish abundance influenced the diets of carnivorous fishes by examining stomach contents of fishes from both basins. Stomach contents were grouped as crayfish, fish, non-crayfish invertebrate, and herpetological. Although the percent occurrence of crayfish in fish stomachs differed between floodplain inundation and low-water periods in the ARB, crayfish were still the major diet constituent of ARB fishes during both periods. Non-crayfish invertebrate was the major diet constituent in BB fishes, with crayfish ranking as the second fewest diet constituent present. Our results demonstrate how flood pulse dynamics influence crayfish, and ultimately trophic webs, in large river-floodplain systems.

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INTRODUCTION

Productivity in many large river-floodplain systems is driven by an annual flood pulse that creates lateral hydrologic connectivity, connects the main river channel to isolated backwater and floodplain habitats, and provides a mechanism of energy and nutrient transfer between the aquatic and terrestrial zones, which enhances biological productivity and supports high levels of fisheries production (Junk et al. 1989; Bayley 1995). Additionally, the spatial and temporal extent of floodplain inundation influences water quality, aquatic species diversity, and overall biomass production in large river-floodplain systems (Junk et al. 1989; Sabo et al. 1999a, 1999b; Lindholm et al. 2007; Gorski et al. 2011; Alford and Walker 2013). Floodplain inundation provides important foraging and spawning opportunities for many fishes (Rutherford et al. 2001; Eggleton et al. 2016) and crayfish (Bonvillain et al. 2013; Kong et al. 2019) that have life history strategies adapted to exploit seasonal flooding periods of large river-floodplains.

Although the timing, magnitude, and duration of the flood pulse varies annually, the Mississippi River typically inundates the adjacent floodplain in the spring and dewaters from summer to early fall. The historic lower Mississippi River floodplain once compromised more than 101,000 km^2, however, anthropogenic modifications for flood protection and navigation have reduced the current floodplain to less than 10% of its historic size (Schramm and Ickes 2016). In Louisiana, levee construction, distributary closures, and flood control structures along the Mississippi River have altered the natural hydrologic regime and disconnected historic floodplains from Mississippi River inputs.

The Atchafalaya River Basin (ARB) and Barataria Basin (BB) in south Louisiana are Mississippi River floodplain systems separated by approximately 25 km (Figure 1). Both basins are characterized by shallow headwater and backwater lakes, cypress-tupelo swamps, and numerous natural bayous and excavated canals. The ARB and BB both historically received waters from the annual Mississippi River flood pulse and shared similar hydrologic regimes. However, anthropogenic modifications have altered the historic connectivity of these basins with the Mississippi River and changed the hydrologic functionality between the basins.

The ARB is approximately 25–35 km wide and is bounded by protection levees that restrict the floodplain to 26% of its historic

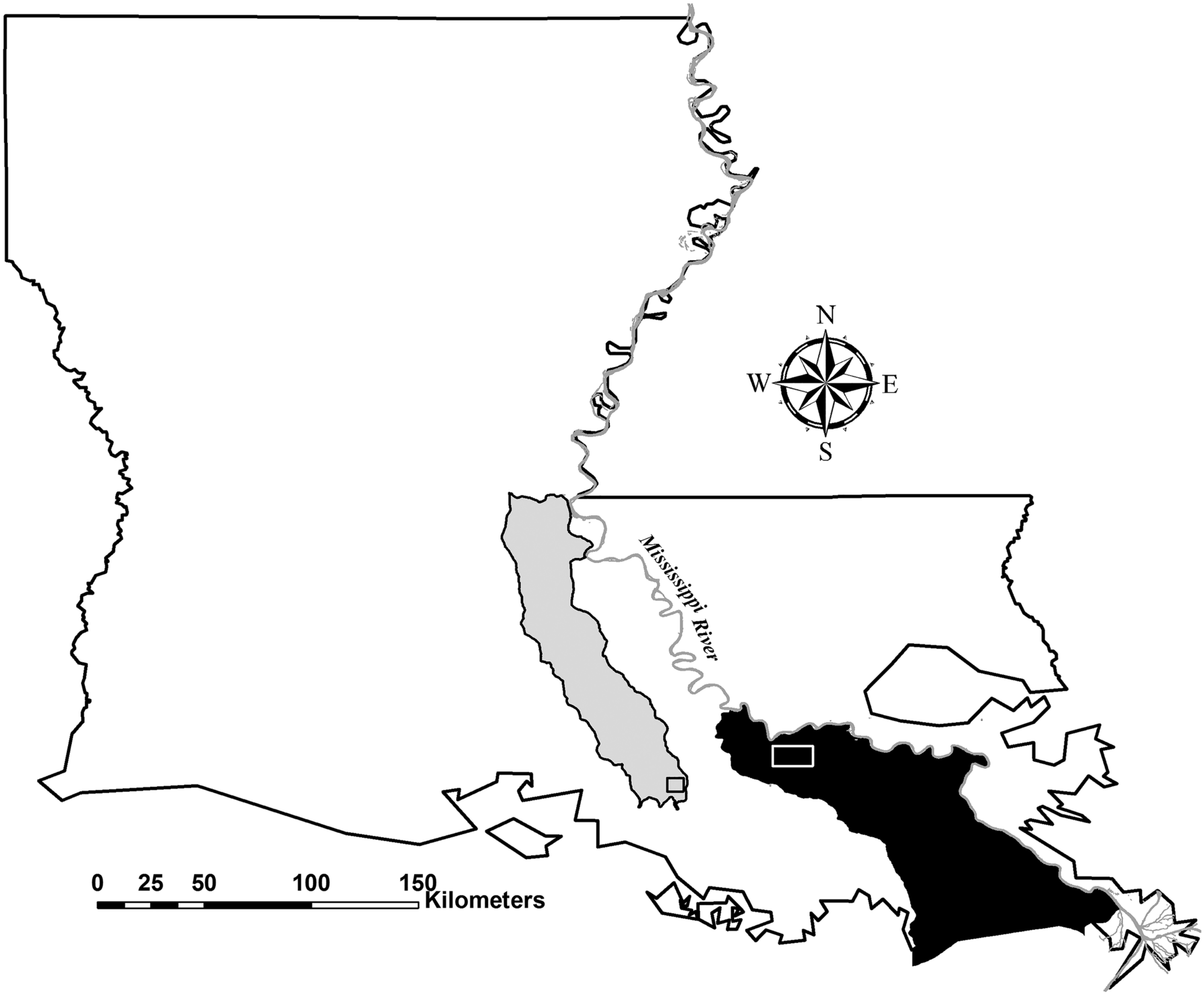

Figure 1. The Atchafalaya River Basin (grey) and Barataria Basin (black) in south Louisiana. Boxes within each basin indicate study area.

range (Ford and Nyman 2011). However, the ARB still receives an annual flood pulse from the Mississippi River through the Atchafalaya River, the major distributary of the Mississippi River. The Atchafalaya River receives 30% of the combined volumes of the Red and Mississippi Rivers through two water control structures and a hydropower channel regulated by the US Army Corps of Engineers. Water levels in the ARB reflect Mississippi River level fluctuations and floodplain inundation typically occurs in the spring with drawdown in summer (Bonvillain et al. 2008). The seasonal floodplain inundation and drawdown provides optimal conditions that coincide with crayfish life history characteristics, specifically red swamp crayfish *Procambarus clarkii* (Girard) and southern white river crayfish *Procambarus zonangulus* (Hobbs and Hobbs), and supports the largest wild crayfish harvest in Louisiana (Bonvillain et al. 2013; Kong et al. 2019).

The BB is the historic southernmost western floodplain of the Mississippi River and historically received an annual flood pulse from the Mississippi River. However, distributary closures and construction of the Mississippi River levee system have decoupled the BB from the Mississippi River and eliminated the annual flood pulse from entering the system. Currently, BB floodplain habitats, located in the most inland reaches of the BB, only become inundated during large or prolonged precipitation events (Nelson et al. 2002). Precipitation-driven floodplain inundation events produce acute inundation events throughout the year that do not necessarily coincide with the life history (i.e., spawning season) of many floodplain dependent species and restricts access to floodplain habitats used by aquatic biota for spawning and forage (Balcombe and Arthington 2009; Ballinger 2018; Rixner 2018). Furthermore, the lack of an annual flood pulse and episodic floodplain inundation events experienced in the BB have diminished *P. clarkii* abundance in this system (Ballinger 2018).

Crayfish are key components in various aquatic trophic webs and are an important dietary constituent in many carnivorous fishes. Both piscivorous fishes including gar, bowfin, crappie, bass, and catfish (Lambou 1961; Ashley and Rachels 1999; Garvey et al. 2003; Sammons 2012; Walker et al. 2013) and insectivorous fishes including bluegill, warmouth, and freshwater drum (Wahl et al. 1988; Roth et al. 2007; Miller et al. 2015) consume crayfish, and depending on habitat characteristics and prey availability, crayfish can comprise a considerable portion of ingested prey (Crowl 1989; Hickley et al. 2002; Rixner 2018). Although crayfish provide less useable caloric content per gram than other invertebrates and fishes, they are likely more energetically important prey items in large river-floodplains because of high densities (Stein 1977; Rabeni 1992).

Seasonal floodplain inundation periods in large river-floodplains drive biotic productivity and influence aquatic trophic web dynamics. The hydrologic regime of the flood pulse affects predator and prey resources and interactions, trophic web energy fluxes, aquatic biota diet composition, and aquatic biota success (Rutherford et al. 2001; de Mérona and Rankin-de-Mérona 2004; Lindholm et al. 2007; Luz-Agostinho et al. 2008; Bonvillain et al. 2013; Kong et al. 2019). Furthermore, floodplain inundation periods provide seasonal variations in food resources and a larger diet breadth for fishes (Balcombe et al. 2005). In the ARB, the annual flood pulse contributes to its high crayfish production (Bonvillain et al. 2013), which produces over 90% of the wild crayfish harvest in Louisiana (Isaacs and Lavergne 2010).

Crayfish can be a major diet component of carnivorous fish in the Mississippi River floodplain system (Miller et al. 2015). Because floodplain inundation from the annual ARB flood pulse provides conditions that support high crayfish abundance, fishes in this system have access to an abundant prey source. Conversely, the absence of an annual flood pulse and consistent seasonal floodplain inundation in the BB has reduced crayfish abundance, an important prey item in floodplain trophic webs, which can lead to diet shifts in many carnivorous fishes (Luz-Agostinho et al. 2008). Therefore, the objective of this study was to determine if the absence of an annual flood pulse and reduced crayfish abundance influenced the diets of carnivorous fishes. Specifically, we examined the stomach contents of fishes from the ARB and BB during multiple research projects and in the ARB during floodplain inundation and low-water periods.

MATERIALS AND METHODS

Fishes examined for this study were collected as a part of three separate research endeavors in the ARB and BB between 2006 and 2018. Study 1 collected fishes monthly in the BB from October 2006 to September 2007, study 2 collected fishes bi-monthly in the ARB from March 2008 to July 2009, and study 3 collected fishes monthly in the ARB and BB from August 2017 to April 2018. Sample locations in all studies were located in natural bayous and excavated canals, and the same locations were sampled during low-water (late summer to winter) and floodplain inundation periods (spring to summer) in the ARB. Fishes in study 1 were collected with 35 mm monofilament gill nets fished for one hour. Fishes in studies 2 and 3 were collected via boat electrofishing with a Smith-Root 7.5 Generator Powered Pulsator electrofisher system. During all three studies, adult carnivorous fishes were placed on ice and transported back to the laboratory for stomach analysis. Whole stomachs were removed, placed into individual labeled Hubco cloth sample bags, and placed into storage containers with 75% ethanol until examination. Stomach contents were identified to the lowest taxonomic group possible, but were grouped into one of four categories: crayfish, fish, non-crayfish invertebrate, or herpetological (reptile or amphibian). Multiple diet categories were recorded present when more than one diet item was present in a fish. Stomach contents data from all studies were pooled by basin for analyses. Chi-square tests were used to examine differences in each diet category between basins. Floodplain inundation in the ARB was determined when the Atchafalaya River stage at Butte La Rose, Louisiana (US Army Corps of Engineers gauge 03120) was greater than 2.5 m and floodplain habitats in the study area began to experience overbank flooding (Bonvillain et al. 2013).

Table 1. Fish species sampled for stomach contents in the Atchafalaya River Basin (ARB) and Barataria Basin (BB).

Species	Common Name	Basin
Ameiurus melas (Rafinesque)	Black bullhead	BB
Ameiurus natalis (Lesueur)	Yellow bullhead	BB
Amia calva Linnaeus	Bowfin	Both
Aplodinotus grunniens Rafinesque	Freshwater drum	ARB
Ictalurus furcatus (Valenciennes)	Blue catfish	Both
Ictalurus punctatus (Rafinesque)	Channel catfish	Both
Lepisosteus oculatus Winchell	Spotted gar	Both
Lepisosteus osseus (Linnaeus)	Longnose gar	ARB
Lepomis gulosus (Cuvier)	Warmouth	Both
Lepomis macrochirus Rafinesque	Bluegill	Both
Lepomis megalotis (Rafinesque)	Longear sunfish	ARB
Lepomis microlophus (Günther)	Redear sunfish	Both
Lepomis punctatus (Valenciennes)	Spotted sunfish	ARB
Micropterus salmoides (Lacepède)	Largemouth bass	Both
Morone chrysops (Rafinesque)	White bass	ARB
Morone mississippiensis Jordan and Eigenmann	Yellow bass	ARB
Pomoxis nigromaculatus (Lesueur)	Black crappie	Both

RESULTS

We examined the stomach contents of 463 and 652 adult carnivorous fishes from the ARB and BB, respectively. In the ARB, 275 and 188 fishes were examined in studies 2 and 3, respectively, and 401 and 251 BB fishes were examined in studies 1 and 3, respectively. Fishes with stomach contents included 210 (45% with contents, 55% empty stomachs) individuals from the ARB and 333 individuals (51% with contents, 49% empty stomachs) from the BB comprising 17 species (Table 1). Crayfish was the major diet constituent in ARB fishes and was found in 61% of individuals with stomach contents. The second most abundant item found in ARB fish stomachs was fish (28%), followed by non-crayfish invertebrates (22%), and herpetological (1%; Figure

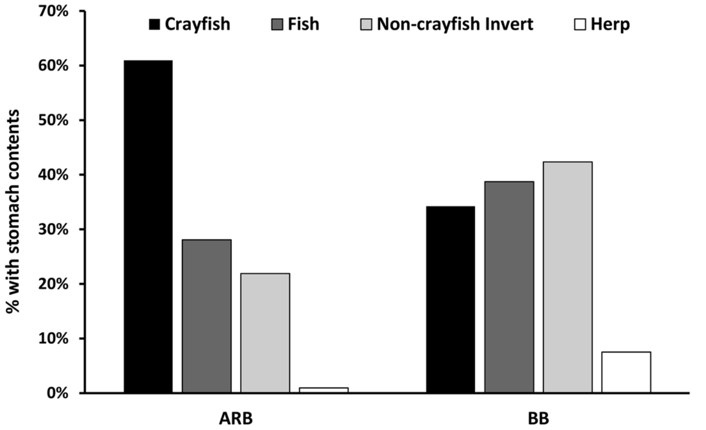

Figure 2. Percent of diet constituents in fishes sampled with stomach contents in the Atchafalaya River Basin (ARB) and Barataria Basin (BB).

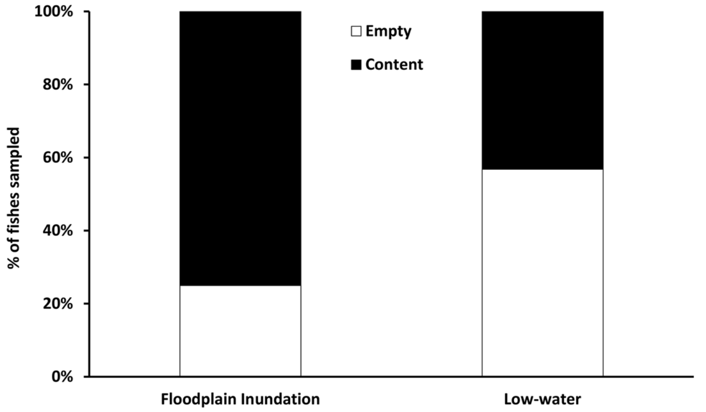

Figure 3. Percent of fishes sampled in the Atchafalaya River Basin with empty stomachs and stomach contents during floodplain inundation and low-water periods.

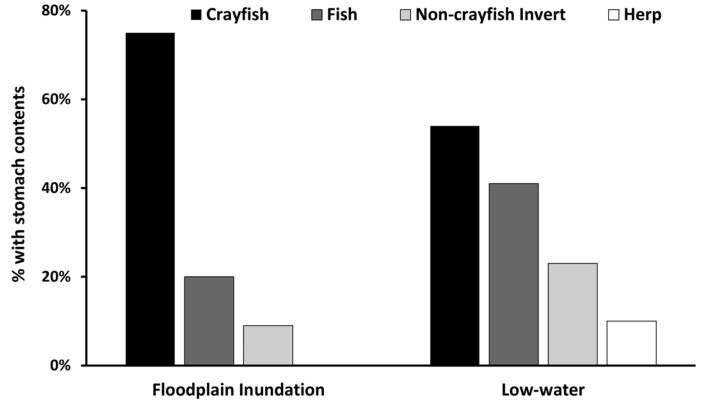

Figure 4. Percent of diet constituents in Atchafalaya River Basin fishes sampled with stomach contents during floodplain inundation and low-water periods.

2). Conversely, with the exception of herpetological (8%), diet constituents of BB fishes exhibited an inverse trend compared to the ARB with non-crayfish invertebrate as the major constituent (42%) followed by fish (39%) and crayfish (34%; Figure 2). Crayfish were significantly more abundant ($\chi^2 = 37.21$, $P < 0.001$) in ARB fish diets compared to BB fishes. Conversely, fish ($\chi^2 = 6.45$, $P = 0.011$), non-crayfish invertebrates ($\chi^2 = 21.02$, $P < 0.001$), and herps ($\chi^2 = 11.71$, $P < 0.001$) were significantly more abundant in BB fish diets compared to ARB fish.

Fish collection efficiency declined during ARB floodplain inundation periods as habitat availability increased and fish presumably moved onto the inundated floodplain for spawning and feeding opportunities (Bonvillain et al. 2008). Forty-four fishes were collected during ARB floodplain inundation periods and 419 fishes were collected during low-water periods for stomach content examination. During floodplain inundation, 75% of fishes sampled had contents in their stomachs, however, less than half of fishes (48%) had stomach contents during low-water periods (Figure 3). Additionally, during floodplain inundation periods, crayfish was the principal diet constituent, found in 75% of fishes with stomach contents followed by fish (20%) and non-crayfish invertebrates (9%; Figure 4). No herpetological stomach contents were found in fishes during floodplain inundation periods. During low-water periods, crayfish was still the main diet constituent (54%) followed by fish (41%), non-crayfish invertebrates (23%), and herpetological (10%; Figure 4).

DISCUSSION

The annual flood pulse is a key component that drives biotic biomass production in large river-floodplain systems and supports the largest wild crayfish harvest in Louisiana. However, the absence of a flood pulse and the different hydrologic regime experienced in the BB influences river-floodplain interaction and ultimately crayfish abundance and the availability of prey resources for fishes (Ballinger 2018). Ballinger (2018) sampled eleven times more crayfish in the ARB compared to the BB during the same temporal period. The large crayfish abundance supported in the ARB provides carnivorous fishes with a food rich environment which can act as a stabilizing force for food web dynamics (Kovalenko 2019).

Crayfish were the major diet constituent of ARB fishes sampled, even during low-water periods. This supports previous ARB fish diet studies that revealed crayfish as a major diet constituent in *Amia calva* (Linnaeus; bowfin), *Lepisosteus oculatus* (Winchell; spotted gar), and centrarchids (Lambou 1961; Dugas et al. 1976; Miller et al. 2015; Rixner 2018). Crayfish are likely a non-limiting floodplain resource in the ARB during floodplain inundation periods, and the abundance of crayfish may benefit fish populations and trophic web stability several ways. The abundance of ARB crayfish provides a prey resource that is the most profitable food resource (Correa and Winemiller 2014) and optimally exploited by fishes (Stein 1977) and is the most energetically important dietary constituent for many fishes (Rabeni 1992). Furthermore, the high abundance of crayfish likely limits competition among fishes and reduces negative consequences of niche overlap (Correa and Winemiller 2014). Lastly, crayfish abundance reduces fish predation on other aquatic animals and increases aquatic trophic web stability and ecosystem resilience (Kovalenko 2019).

Floodplain inundation is an environmental cue for crayfish to emerge from burrow habitats and provides peak crayfish abundance periods in the ARB (Bonvillain et al. 2013; Kong et al. 2019). Fish consume different prey resources in frequencies that are influenced by hydrological seasonality (Correa and Winemiller 2014). This was evident during floodplain inundation periods when crayfish abundance was high and 75% of fishes with stomach contents contained crayfish, and 75% of the total fishes sampled contained stomach contents. Dugas et al. (1976) observed similar trends in *Amia calva* sampled in the ARB. During floodplain inundation periods, crayfish provide a prey resource pulse that likely contributes to an opportunistic change in carnivorous fish foraging behavior (Balcombe et al. 2005; Kovalenko 2019). Although the amount of crayfish present in fish stomachs decreased and fish, non-crayfish invertebrates, and herps increased during low water periods, crayfish was still the major diet constituent in carnivorous fishes sampled. Most *P. clarkii* and *P. zonangulus* will retreat to burrows as water levels recede from the floodplain, however, individuals can still be found in wetted areas throughout the year (Bonvillain 2012). However, variation in carnivorous fish diets occurred as food resources changed and water levels and crayfish resource availability decreased. During low-water periods, dietary shifts were evident as fishes consumed more fish, non-crayfish invertebrate, and herpetological resources with only a little more than half of the fishes sampled (52%) that contained stomach contents, similar to results observed by other ARB dietary studies (Lambou 1961; Dugas et al. 1976). Dietary shifts in fishes are common in river-floodplain systems as the availability of habitat and food resources decline during low-water periods (de Mérona and Rankin-de-Mérona 2004; Balcombe et al. 2005; Grosholz and Gallo 2006; Luz-Agostinho et al. 2008; Correa and Winemiller 2014).

The absence of an annual flood pulse in the BB reduces aquatic and terrestrial zone interactions, which results in negative impacts to aquatic biota, including reduced spatial habitat heterogeneity, greater temporal instability, restriction to floodplain resources, reduced energy inputs to fish production, and asynchrony between life history characteristics and floodplain inundation (Lindholm et al. 2007; Eggleton et al. 2016). The acute, asynchronous floodplain inundation regime experienced in the BB has reduced fish reproduction (Davis 2006; Rixner 2018) and crayfish abundance and individual size (Ballinger 2018). Although diminished fish reproductive success and prey resources have been observed in the BB, the BB and ARB still share similar fish assemblages (Wallace 2018). Additionally, reductions in floodplain inundation and connectance in the lower Mississippi River have resulted in few fish species extinctions (Eggleton et al. 2016). However, the reduced crayfish abundance in the BB has potentially altered the trophic dynamics in this system. Food consumption of fishes in the BB (51% of fishes sampled contained stomach contents) was comparable to low-water periods in the ARB (43%). Additionally, the percent of fish found in BB fish stomach contents (39%) was similar to fishes in the ARB during low-water periods (41%). However, it appears that BB fishes alter their feeding behavior and ingest more non-crayfish invertebrate and herpetological prey resources to compensate for reduced crayfish availability. Shifts in BB fish diets, compared to the ARB, can increase predation on other trophic groups and impact prey populations (Grosholz and Gallo 2006) and increase competition through diet overlap (Luz-Agostinho et al. 2007).

Although there are inherent limitations in the stomach content data presented in this paper, e.g., fishes collected with both active and passive sampling techniques and during different temporal periods, it provides a broad representation of carnivorous fish diets in the ARB and BB. Gear type can influence presence or absence of fish stomach contents through differences in regurgitation or bias towards actively foraging individuals (Hayward et al. 1989; Sutton et al. 2004; Garvey and Chipps 2012). However, the current study does not compare presence/absence of fish stomach contents between basins but simply examines diet composition in fishes with stomach contents present, which the authors consider was not influenced by gear type from extensive sampling experience. Additionally, flood pulse dynamics can affect crayfish abundance and fish community structure in the ARB and BB (Bonvillain et al. 2013; Grosch 2015; Ballinger 2018; Kong et al. 2019). However, both basins experienced basin-specific, typical hydrologic regimes (Bonvillain et al. 2008; Ballinger 2018) during all three temporal periods examined in this study, and fish diet composition is likely representative of both basins during most years. Additionally, although water quality fluctuates spatially and temporally in both basins, physicochemistry, including dissolved oxygen and salinity, at sample areas within the ARB and BB are similar (Bonvillain et al. 2013; Eddlemon and Boopathy 2013; Ballinger 2018; Rixner 2018; Wallace 2018). Finally, it should be noted that diet composition may be biased for crayfish as exoskeleton remains take longer to digest and fish larvae are rapidly digested by many fishes (Kim and DeVries 2001; Garvey and Chipps 2012).

The high crayfish abundance in the ARB provides fishes with a presumably non-limiting food resource, particularly during floodplain inundation periods, and reduces dependence on other aquatic prey organisms. Fishes typically have more specialized diets when resources, such as crayfish, are abundant and broaden their diets during periods of reduced food availability, e.g., ARB low-water periods and the BB (Correa and Winemiller 2014). Aquatic trophic webs change in response to anthropogenic habitat alterations (Kovalenko 2019), and the elimination of the annual flood pulse in the BB has reduced crayfish abundance and potentially altered the trophic dynamics in this system. Pre-levee construction biotic and abiotic empirical data in the BB is sparse and it is impossible to know what the diet composition of BB fishes looked like before hydrologic modifications. However, many of the biotic and abiotic differences observed between the ARB and BB are directly or indirectly attributed to the different hydrologic regimes/flood pulse characteristics experienced in both basins (Reed 1995; Grosch 2015; Ballinger 2018; Rixner 2018; Wallace 2018). Our results demonstrate the importance of crayfish as a diet constituent in carnivorous fishes and the potential consequences of anthropogenic hydrologic modifications on trophic webs in the BB. This information is critical to stakeholders and resource managers as restoration projects to improve water flow in the ARB and reintroduce Mississippi River waters in the BB move forward (Piazza 2014; CPRA 2017).

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