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Comparisons of oxbow lake fish assemblages in relation to bigheaded carp establishment in the lower White River, Arkansas

Michael A. Eggleton^{1*}, Cody J. Salzman¹, Joseph E. Kaiser² and Shannon C. F. Smith³

Abstract

Background Since the late 1990s, bigheaded carps (largely silver carp [*Hypophthalmichthys molitrix*] but also bighead carp [*H. nobilis*]) have established throughout the lower Mississippi River basin. Using previously studied oxbow lakes in the lower White River basin, Arkansas, we compared current (2017, “post-carp” establishment) fish assemblages to historical (2002, “pre-carp” establishment) fish assemblages. Fish assemblages were comprehensively assessed using multiple gears, including boat electrofishing, mini-fyke nets, and experimental small-mesh gill nets.

Results *T*-tests suggested that fish assemblage indices of richness, diversity, evenness, and dominance were often greater ($P < 0.05$) during the post-carp period as reflected by boat electrofishing and experimental gill nets. However, all indices were generally similar ($P > 0.05$) between the pre-carp and post-carp period with fish assemblages depicted using mini-fyke nets. Nonmetric multidimensional scaling analyses indicated that fish assemblages differed structurally between pre-carp and post-carp periods. Assemblage differences were linked to both small and large abundance changes for more than 20 species. Abundances of gizzard shad (*Dorosoma cepedianum*), emerald shiner (*Notropis atherinoides*), pugnose minnow (*Opsopoeodus emiliae*), crappies (*Pomoxis* spp.), bluegill (*Lepomis macrochirus*), orangespotted sunfish (*L. humilis*), and yellow bass (*Morone mississippiensis*) declined between the pre-carp and post-carp periods. Conversely, abundances of weed shiner (*N. texanus*), pallid shiner (*Hybopsis amnis*), longear sunfish (*L. megalotis*), buffalofishes (*Ictiobus* spp.), and gars (*Lepisosteus* spp.) generally increased during the same period.

Conclusions Although not possible to conclude assemblage shifts were entirely related to bigheaded carps due to the absence of an appropriate reference system where carps did not establish, the wide establishment of these carps is one of the most pervasive changes to have occurred in the lower White River ecosystem during the past two decades. Thus, it is probable to conclude that post-carp establishment observations from this study were at least, in part, attributable to bigheaded carp establishment. Impacts of further range expansions by bigheaded carps in the White River and other lower Mississippi River sub-basins are unclear, though this study suggests probable effects on native fish assemblages, underscoring the need for further research and monitoring.

Keywords Bigheaded carp, Silver carp, Aquatic nuisance species, Fish assemblage, Oxbow lake, Large river

*Correspondence:

Michael A. Eggleton
eggletonm@uapb.edu

¹ Department of Aquaculture and Fisheries, University of Arkansas at Pine Bluff, 1200 North University, Box 4912, Pine Bluff, AR 71601, USA

² Arkansas Game and Fish Commission, 650 South Street, Mountain Home, AR 72653, USA

³ Virginia Institute of Marine Science, 1375 Greate Road, Gloucester Point, VA 23062, USA

Background

Bigheaded carps (silver carp [*Hypophthalmichthys molitrix*] and bighead carp [*H. nobilis*]) were first imported to the USA by a commercial fish producer in Arkansas in 1973 (Kelly et al. 2011). Initially, these species were assessed as biological control agents to improve water quality and for their suitability for commercial

aquaculture production (Conover et al. 2007). These fish were soon transferred over to the Arkansas Game and Fish Commission (AGFC) for further research, where they were successfully spawned and studied for a decade. In 1975, the first report of bigheaded carps in the wild came from Crooked Creek within the White River basin in Arkansas County, Arkansas (Kolar et al. 2005). Freeze and Henderson (1982) reported scattered catches of adult bigheaded carps in the Arkansas and White river basins by 1980, though they did not distinguish species. During the 1970s and 1980s, research with bigheaded carps was conducted by at least six state and federal agencies and three universities in seven states (Kelly et al. 2011). By the 1980s, both carps had been introduced or escaped into Alabama, Arizona, Arkansas, Illinois, and Tennessee waters (Chapman and Hoff 2011). During the 1990s and 2000s, rapid population increases and range expansions coincided with several years of excessive flooding in the lower Mississippi River and its tributaries, which included the White River (Kelly et al. 2011). Although the exact pathway of bigheaded carps into the wild cannot be pinpointed, it is most probable that they escaped from multiple locations at different times and expanded from sites where they had been introduced.

By 2000, the rapid and widespread expansion of bigheaded carps had gained national attention and heightened concerns over their potential impacts on native fish assemblages and fisheries (Conover et al. 2007). By 2005, bigheaded carps were recorded from within or along the borders of at least 23 states, with self-sustaining populations existing in the Mississippi, Missouri, Ohio, and Tennessee river basins (Kolar et al. 2005; Schofield et al. 2005; Nico et al. 2016a, b). Multiple studies have attributed ecological, economic, and human health-related impacts to bigheaded carps (e.g., Rogowski et al. 2009; Irons et al. 2011; Pendleton et al. 2017; DeBoer et al. 2018; Love et al. 2018; Chick et al. 2020). Potential management alternatives were developed and proposed through a multi-agency national management plan (Conover et al. 2007). Recent studies over the last decade have emphasized bigheaded carp ecology and their potential impacts in the wild (e.g., Solomon et al. 2016; Pendleton et al. 2017; Phelps et al. 2017; Pyron et al. 2017; Chick et al. 2020; Broaddus and Lamer 2022), and the feasibility for management, control, and/or eradication (e.g., Gutierrez and Teem 2006; O'Connell et al. 2011; Tsehaye et al. 2013; Seibert et al. 2015).

In Arkansas, USA, bigheaded carps have been present for more than 30 years and well-established in several river basins for at least 10 years. In the lower White River in eastern Arkansas, various natural resource agencies and managers confirm that bigheaded carps (mostly silver carp) have become established during the

past 15 years, with substantial increases in abundance occurring around 2008–2010 (A. Hitchcock, U.S. Fish and Wildlife Service, personal communication). Prior to this period in 2002, comprehensive fish assemblage data using multiple sampling gears (boat electrofishing, mini-fyke nets, and experimental small-mesh gill nets) were collected from 16 oxbow lakes in the lower White River system (Lubinski et al. 2008; Eggleton et al. 2010). This study collected only one silver carp and no bighead carp. In a related White River study conducted in 2004–2005, Clark (2006) also reported capturing one silver carp from a study that included over 40 floodplain lakes. During this same period, there were no reports from anglers, boaters, hunters, or biologists of large schools of bigheaded carps, one species of which is noted for its conspicuous “jumping” behavior. However, by the period 2010–2014, large schools of “jumping carps” (presumably silver carp) were being commonly reported in the lower White River basin and its floodplain lakes. Thus, it is certain that bigheaded carps are currently well-established throughout the lower White River basin, with the establishment being most pronounced about 2008–2010.

Given the timing of the Lubinski et al. (2008) and Clark (2006) studies and subsequent establishment of bigheaded carps in the years after, a unique opportunity existed to examine possible bigheaded carp effects on native fish assemblages, using lower White River oxbow lakes as study systems. The goal of this research was to examine changes in fish assemblages in lower White River oxbow lakes between two discrete time periods—2002 and 2017. The first time period (2002) was well-documented to have preceded widespread establishment of bigheaded carps while the second time period (2017) occurred up to a decade post-establishment. Thus, the objectives of this study were to:

1. Compare current (2017, post-carp establishment) oxbow lake fish assemblage measures (i.e., richness, diversity, evenness, and dominance) to those collected from historical datasets (2002, pre-carp establishment), and
2. Compare current oxbow lake fish assemblage species compositions to those measured historically using multivariate statistical techniques.

Historical datasets collected during 2002 will herein be termed “pre-carp” while the current study (2017) will be termed “post-carp.” Although any effects detected could never unequivocally be linked to bigheaded carps due to the absence of an appropriate reference system that did not experience carp establishment, results have great potential to shed light on possible effects that these

invasive carps may be having on native fishes and fisheries as their ranges continue to expand in Arkansas and other USA rivers.

Methods

Study area

The lower White River, Arkansas is one of the more natural lowland river-floodplain ecosystems in the USA (Lubinski et al. 2008). Located downstream of Batesville, Arkansas, this river reach is relatively unregulated and contains an active floodplain. A large portion of the ecosystem is contained within the federally protected, U.S. Fish and Wildlife Service managed Dale Bumpers White River National Wildlife Refuge (WRNWR), which is located downstream of river km (RKM) 161 at Clarendon, Arkansas (Lubinski et al. 2008). The WRNWR contains roughly 360 floodplain lakes larger than 2 ha that vary in morphology, connectivity, and accessibility located within approximately 65,000 ha of bottomland hardwood forest floodplain habitat. The refuge also contains hundreds of smaller lakes and interconnected sloughs and bayous. Seasonal flood pulses are the primary mechanism by which these floodplain lakes become seasonally connected to the White River main-stem (Lubinski et al. 2008). Seasonal flooding in the refuge is affected both by the White River and several larger tributaries upstream and backflows from the lower Mississippi River main-stem downstream. State management biologists consider floodplain lake fisheries within the WRNWR as among the most significant sport fisheries in eastern Arkansas (J. Homan, AGFC, personal communication).

Fifteen WRNWR oxbow lakes that were studied historically were selected for this study (Fig. 1). These 15 lakes were considered representative of all oxbow lakes in that they were distributed throughout the refuge and contained a variety of flooding characteristics, including lakes that were frequently, moderately, and rarely connected to the White River main-stem by annual flooding. Study lakes averaged 21.4 ± 3.7 ha in surface area (range 2.8–48.1 ha) and averaged 2.3 ± 0.3 m in depth (range 1.2–4.7 m) (Lubinski et al. 2008). These statistics were similar to those from another study by Clark et al. (2007), which studied a larger sample of WRNWR oxbow lakes 2–3 years later. Lubinski et al. (2008) contains additional information concerning lake characteristics. A sixteenth lake (East Moon Lake) studied by Lubinski et al. (2008) and Clark et al. (2007) was excluded from the current study due to access issues that had arisen during the intervening period between studies.

Fish collections

Oxbow lake fish assemblages were sampled with the same gears and effort levels, and during the same seasons

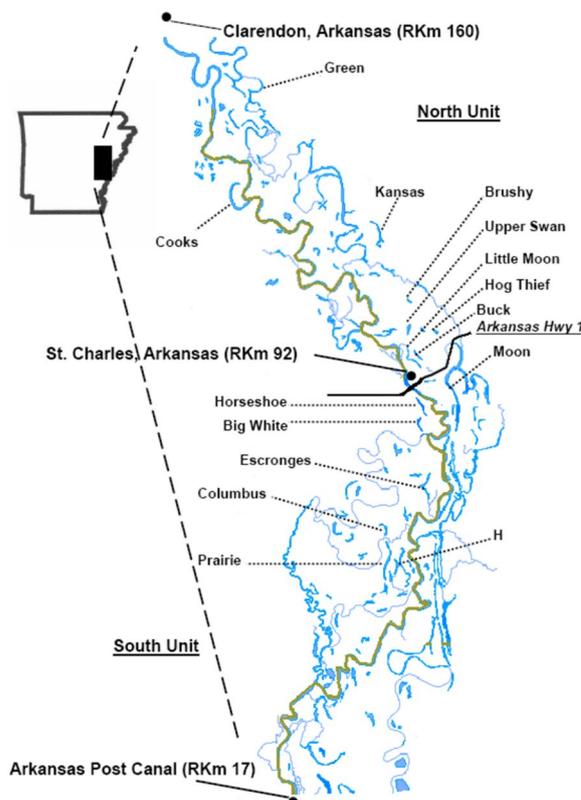


Fig. 1 Fifteen oxbow lakes sampled in the White River National Wildlife Refuge of the lower White River basin. Scale: 1 cm = 2 km (1 inch = 5 miles). Map borrowed from Lubinski et al. (2008). A sixteenth lake (East Moon Lake) sampled by Lubinski et al. (2008) was not included in this study due to logistical issues that arose between 2002 and 2017

as used by Lubinski et al. (2008). Gear types used were mini-fyke nets, experimental small-mesh gill nets, and boat-mounted electrofishing. All 2017 sampling was conducted during summer (July–August) and fall (October–November) following the same design used in 2002. In each lake, four modified mini-fyke nets were fished concurrently during summer for approximately 24 h each. Mini-fyke nets had a 3-mm bar mesh size; the frame was constructed of two rectangles 0.6 m × 1.2 m made of 7.9 mm black oil-tempered spring steel. The net lead was 4.5 m long × 0.6 m high with floats every 91.4 cm and lead weights along the bottom every 30.5 cm. Nets were coated in green latex dip to prevent weathering. Other mini-fyke net specifications were identical to those used by Lubinski et al. (2008).

Three monofilament experimental small-mesh gill nets were fished in each lake during summer 2017. Gill nets were fished for 4 h each in conjunction with the retrieving of mini-fyke nets, being set in the morning from approximately 08:00 to 12:00. Nets had five different equal-area mesh sizes to reduce fish size

selectivity (Hubert et al. 2012). Gill nets were 38.1 m in length and 2.4 m deep, with mesh sizes of 2.54-, 3.81-, 5.08-, 6.35-, and 7.62-cm square mesh. A perpendicular net set was conducted with the 2.54-cm mesh end of each fished nearest to shore and the net anchored at both ends; net ends were marked with floats. All other experimental gill net specifications were identical to those used by Lubinski et al. (2008).

Boat-mounted electrofishing was conducted during daytime at randomly selected locations in each lake using a pulsed-DC Smith-Root 7.5 GPP electrofisher (Smith-Root; Vancouver, Washington, USA) during fall. Six, 10-min samples (three at 1000-V/15-Hz, three at 500-V/60-Hz; Lubinski et al. 2008) were taken in each lake. Electrofishing output settings were standardized based on water temperature and conductivity to achieve a standard power output of approximately 3000–3500 W in all lakes (Burkhardt and Gutreuter 1995). Samples were taken with two dip-netters using a 2.4-m long fiberglass dip net pole with a Smith-Root heavy-duty style net. All collected fishes were identified to species in the field and released alive. When field identification was not possible (e.g., small-bodied and/or juvenile cyprinids, percids, and lepidomids), fishes were preserved in 90% ethanol, labeled, and returned to the laboratory for identification using standard taxonomic keys (e.g., Pflieger 1997; Robison and Buchanan 2020). All electrofishing equipment and other specifications were identical to those used by Lubinski et al. (2008), except that previous (2002) electrofishing had been conducted during nighttime hours. The possibility of daytime vs. nighttime electrofishing differences was considered, though not judged to be significant given the size and depth characteristics of the study lakes. Although previous studies (e.g., Paragamian 1989; Sanders 1992; Pierce et al. 2001; Dumont and Dennis 2011) have demonstrated daytime-nighttime differences with respect to catch-per-unit-effort and size structure of some sportfish species, assemblage differences are not usually encountered in littoral zones of smaller, shallower systems such as the oxbow lakes used in this study. During subsequent work conducted in WRNWR lakes in 2004–2005, Clark (2006) reported that richness, diversity, and evenness values generated from boat electrofishing in these same lakes did not differ between daytime and nighttime periods, which prompted their decision to continue with daytime-only boat electrofishing sampling. Although more recent studies (e.g., Bouska et al. 2017; Hammen et al. 2019) have modified existing gears to better target bigheaded carps, we did not add gears more efficient at collecting carps given that our experimental design called for direct comparisons to historical data.

Fish assemblage measures

Following collection, laboratory processing, and identification of all fishes, several common measures of ecological significance were computed. Specifically, species richness, species diversity, species evenness, and species dominance were computed for each gear and lake using standard methods (Washington 1984; Magurran 2004). “Species richness” (S) was defined as the number of species collected from a given sample at a given location. “Menhinick’s Index” (M) also was calculated to standardize richness values by the number of specimens in the collection as:

$$M = \frac{S}{\sqrt{N}}$$

where S equals the number of species present in a sample and N equals the total number of individuals in a sample (Bandeira et al. 2013). “Species diversity” was calculated using the Shannon-Wiener diversity index (H') calculated as:

$$H' = - \sum_{i=1}^s \left(\frac{n_i}{N} \right) \ln \left(\frac{n_i}{N} \right)$$

where S equals the number of species in the sample, n_i equals the number of individuals of species i , and N is the total number of individuals in the sample (Washington 1984). Theoretical maximum species diversity for H' (as H'_{\max}) was similarly estimated as $\ln S$. “Species evenness” (E) reflects how the abundance or biomass of an assemblage is distributed among its component species, and was calculated as:

$$E = \frac{\overline{H'}}{\ln S}$$

where $\overline{H'}$ equals the Shannon-Wiener index value and S equals species richness (Magurran 2004). “Species dominance” was calculated using Simpson’s Dominance index (D), which places greater emphasis on common rather than rare species (Magurran 2004). This index scales from zero (i.e., no species diversity) to one (high species diversity), and was calculated as:

$$D = 1 - \sum \left(\frac{n_i}{N} \right)^2$$

where n_i equals the number of species i and N equals the total number of individuals in the sample (Washington 1984). Values generated from this index also were equivalent to the probability of two random individuals from the sample in question being different species.

Current (2017, post-carp) fish assemblage measures were compared to historical (2002, pre-carp) assemblages

by gear type and with all gears pooled using two-sample two-tailed t -tests that assumed unequal variances (Zar 1999). To remove any potential effects they might have been having on fish assemblage structures, both big-headed carp species were excluded from these analyses following Solomon et al. (2016). All computations and comparisons were conducted using either the data analysis utility in Microsoft Excel for Office 365 (Microsoft Corporation; Redmond, Washington, USA) or the Statistical Analysis Software (SAS), V.9.4 (SAS Institute, Inc. 2013). The alpha (α) level used for all t -tests was 0.05.

Fish assemblage structure

Multivariate ordination was used to examine overall fish assemblage species compositional differences between the pre-carp and post-carp periods in oxbow lakes. Specifically, nonmetric multidimensional scaling (NMS) using a Sørensen (Bray–Curtis) dissimilarity measure (McCune and Grace 2002; Peck 2016) was conducted separately for each gear, with pre-carp and post-carp datasets pooled in the same matrix. As before, both big-headed carp species were removed from ordinations to remove any possible effects they may have had on fish assemblage structures (Solomon et al. 2016). Additionally, because rare species or species with improbable distributions can distort multivariate ordinations to the point of being uninterpretable, exploratory analyses were conducted to screen potential outlying species. From this analysis, one species (paddlefish *Polydon spathula*) represented by a single individual was excluded from the electrofishing dataset. In addition, the catches of two other species were adjusted to prevent their observed catches, which appeared to be aberrant, from distorting analyses. In the mini-fyke net dataset, a single net catch of 14,868 Mississippi silvery minnow (*Hybognathus nuchalis*) estimated from subsampling in 2002 was adjusted to the mean catch for that species across the remaining 14 lakes (6 individuals/lake). In the experimental gill-net dataset, one catch of 16 skipjack herring (*Alosa chrysochloris*) from one lake in 2002 was adjusted to the mean catch for that species across the remaining 14 lakes (1 individual/lake). In both instances, the adjustments made insured that each species was represented in the assemblage, but in more realistic abundances that did not disproportionately distort analyses. Overall, the number of fish species included in each NMS analysis was 63 for electrofishing, 52 for mini-fyke nets, and 29 for experimental gill nets. For each NMS analysis, dimensionality was evaluated and chosen to minimize stress, with interpretations made if final stress values were < 20 (McCune and Grace 2002; Peck 2016). Additionally, pre-carp and post-carp fish assemblage ordinations were compared by gear as two discrete assemblages using multi-response permutation

procedures (MRPP; Cai 2006). Statistical significance for all NMS and MRPP analyses was set at an alpha level of 0.05. All NMS analyses and significance testing were performed using the program PC-ORD, V.7.08 (MJM Software, Gleneden Beach, Oregon, USA). Table 1 contains a list of all fish species collected along with their scientific names, four-letter codes used in NMS ordinations, and their relative abundances during pre-carp and post-carp sampling pooled across all three gears.

Results

Bigheaded carp abundances

During the pre-carp period, no bigheaded carps were captured from electrofishing compared to 48 silver carp and one bighead carp during the post-carp period (Table 1). Post-carp bigheaded carp catch-per-unit-effort was highly variable across all 15 study lakes, averaging 3.2 ± 1.6 (SE) fish/h while ranging from 0.0–24.0 fish/h (Kaiser 2019). Despite the zero catch-per-unit-effort values from some lakes, bigheaded carps were observed in all 15 study lakes. During the 2017 electrofishing that collected 48 bigheaded carps, video-recording of sampling in all lakes documented 621 additional individuals encountered during sampling that were not recovered due to their high numbers and jumping behaviors (Kaiser 2019). Irrespective of gears, Cooks, Prairie, Kansas, and Escronges lakes consistently ranked as lakes with the greatest carp abundances while Upper Swan, Brushy, Horseshoe, and Big White lakes consistently ranked as lakes with the lowest carp abundances. All other lakes ranked as intermediate carp abundances, though some gear-related variation was observed. Overall, 1,978 different bigheaded carps were observed in study lakes during the post-carp period through sampling, video-recording of sampling, and ancillary sampling being done for other purposes.

Gear-specific fish abundances

Given the design of this study (i.e., same lakes, gears, and effort levels expended 15 years apart), direct comparisons of species' numbers, richness, and relative abundances were valid and interpretable. During 2017 sampling in lower White River oxbow lakes, 24,786 fishes representing 67 species were collected compared to 26,348 fishes from 61 species during 2002 (Table 2). These figures suggested that overall sampling efficiencies and gear effectiveness were similar between the pre-carp and post-carp periods. Although it was not possible to have the same sampling crews in both 2002 and 2017, we were able to use the same electrofishing equipment.

Boat electrofishing collected 10,672 fishes that included 58 species during the post-carp period compared to 7500 fishes composed of 46 species collected during

Table 1 Alphabetical listing of fish species collected from multiple-gear fish surveys in lower White River oxbow lakes in 2002 and 2017

Fish code	Common name	Scientific name	2002 Total number (% Composition)	2017 Total number (% Composition)
AGGR	Alligator Gar	<i>Atractosteus spatula</i>	0	1 (<0.1)
BHCP	Bighead Carp	<i>Hypophthalmichthys nobilis</i>	0	1 (<0.1)
BHMW	Bullhead Minnow	<i>Pimephales vigilax</i>	0	42 (0.2)
BKBF	Black Buffalo	<i>Ictiobus niger</i>	34 (0.1)	135 (0.5)
BKCARP	Black Carp	<i>Mylopharyngodon piceus</i>	0	1 (<0.1)
BKCP	Black Crappie	<i>Pomoxis nigromaculatus</i>	124 (0.5)	70 (0.3)
BKSS	Brook Silverside	<i>Labidesthes sicculus</i>	1,724 (6.3)	521 (2.1)
BLCF	Blue Catfish	<i>Ictalurus furcatus</i>	1 (<0.01)	2 (<0.1)
BLGL	Bluegill	<i>Lepomis macrochirus</i>	2,555 (9.4)	2,047 (8.3)
BMBF	Bigmouth Buffalo	<i>Ictiobus cyprinellus</i>	55 (0.2)	251 (1.0)
BNDR	Bluntnose Darter	<i>Etheostoma chlorosomum</i>	61 (0.2)	204 (0.8)
BNMW	Bluntnose Minnow	<i>Pimephales notatus</i>	0	2 (<0.1)
BPSF	Banded Pygmy Sunfish	<i>Elassoma zonatum</i>	11 (<0.1)	1 (<0.1)
BPTM	Blackspotted Topminnow	<i>Fundulus olivaceus</i>	46 (0.2)	137 (0.6)
BSDR	Blackside Darter	<i>Percina maculata</i>	9 (<0.1)	15 (0.1)
BTSN	Blacktail Shiner	<i>Cyprinella venusta</i>	8 (<0.1)	77 (0.3)
BTTM	Blackstripe Topminnow	<i>Fundulus notatus</i>	9 (<0.1)	8 (<0.1)
BWFN	Bowfin	<i>Amia calva</i>	21 (0.1)	56 (0.2)
CARP	Common Carp	<i>Cyprinus carpio</i>	43 (0.2)	64 (0.3)
CNCF	Channel Catfish	<i>Ictalurus punctatus</i>	83 (0.3)	60 (0.2)
CNLP	Chestnut lamprey	<i>Ichthyomyzon castaneus</i>	1 (<0.1)	0
CYDR	Cypress Darter	<i>Etheostoma proeliare</i>	0	51 (0.2)
CYMW	Cypress Minnow	<i>Hybognathus hayi</i>	194 (0.7)	173 (0.7)
DLSF	Dollar sunfish	<i>Lepomis marginatus</i>	57 (0.2)	0
DYDR	Dusky Darter	<i>Percina sciera</i>	1 (<0.1)	29 (0.1)
ERSN	Emerald Shiner	<i>Notropis atherinoides</i>	5,919 (21.8)	2,002 (8.1)
FHCF	Flathead Catfish	<i>Pylodictis olivaris</i>	11 (<0.1)	22 (0.1)
FLIR	Flier	<i>Centrarchus macropterus</i>	0	1 (<0.1)
FWDM	Freshwater Drum	<i>Aplodinotus grunniens</i>	385 (1.4)	393 (1.6)
GDSN	Golden Shiner	<i>Notemigonus crysoleucas</i>	66 (0.2)	30 (0.1)
GDYE	Goldeye	<i>Hiodon alosoides</i>	0	2 (<0.1)
GNSF	Green Sunfish	<i>Lepomis cyanellus</i>	1 (<0.1)	5 (<0.1)
GSCP	Grass Carp	<i>Ctenopharyngodon idella</i>	0	3 (<0.1)
GSPK	Grass Pickerel	<i>Esox americanus</i>	1 (<0.1)	0
GZSD	Gizzard Shad	<i>Dorosoma cepedianum</i>	1,548 (5.7)	609 (2.5)
HFCS	Highfin Carpsucker	<i>Carpiodes velifer</i>	1 (<0.1)	0
LESF	Longear Sunfish	<i>Lepomis megalotis</i>	270 (0.6)	2,487 (10.1)
LGPH	Logperch	<i>Percina caprodes</i>	175 (0.4)	59 (0.2)
LKCS	Lake Chubsucker	<i>Erimyzon sucetta</i>	4 (<0.1)	0
LMBS	Largemouth Bass	<i>Micropterus nigricans</i>	261 (1.0)	410 (1.7)
LNDR	Longnose Gar	<i>Lepisosteus osseus</i>	30 (0.1)	138 (0.6)
MDDR	Mud Darter	<i>Etheostoma asprigene</i>	11 (<0.1)	17 (0.1)
MMSN	Mimic Shiner	<i>Notropis volucellus</i>	1,295 (4.8)	1,834 (7.4)
MQTF	Western Mosquitofish	<i>Gambusia affinis</i>	18 (0.1)	38 (0.2)
NSTM	N. Starhead Topminnow	<i>Fundulus dispar</i>	5 (<0.1)	0
OSSF	Orangespotted Sunfish	<i>Lepomis humilis</i>	947 (3.5)	652 (2.6)
PDFH	Paddlefish	<i>Polyodon spathula</i>	0	1 (<0.1)

Table 1 (continued)

Fish code	Common name	Scientific name	2002 Total number (% Composition)	2017 Total number (% Composition)
PDSN	Pallid Shiner	<i>Hybopsis amnis</i>	27 (0.1)	450 (1.8)
PGMW	Pugnose Minnow	<i>Opsopoeodus emiliae</i>	3,242 (11.9)	285 (1.1)
PRPH	Pirate Perch	<i>Aphredoderus sayanus</i>	22 (0.1)	10 (<0.1)
RESF	Redear Sunfish	<i>Lepomis microlophus</i>	167 (0.6)	159 (0.6)
RVCS	River Carpsucker	<i>Carpionodes carpio</i>	18 (0.1)	3 (<0.1)
RVDR	River Darter	<i>Percina shumardi</i>	0	1 (<0.1)
SGER	Sauger	<i>Sander canadensis</i>	7 (<0.1)	0
SHRH	Shorthead Redhorse	<i>Moxostoma macrolepidotum</i>	2 (<0.1)	1 (<0.1)
SJHR	Skipjack Herring	<i>Alosa chrysochloris</i>	22 (<0.1)	2 (<0.1)
SLDR	Slough Darter	<i>Etheostoma gracile</i>	25 (<0.1)	9 (<0.1)
SMBF	Smallmouth Buffalo	<i>Ictiobus bubalus</i>	189 (0.7)	517 (2.1)
SNGR	Shortnose Gar	<i>Lepisosteus platostomus</i>	30 (0.1)	67 (0.3)
SPSK	Spotted Sucker	<i>Minytrema melanops</i>	125 (0.5)	32 (0.1)
STBS	Spotted Bass	<i>Micropterus punctulatus</i>	131 (0.5)	192 (0.8)
STGR	Spotted Gar	<i>Lepisosteus oculatus</i>	187 (0.7)	257 (1.0)
STSM	Redspotted Sunfish	<i>Lepomis punctatus</i>	4 (<0.1)	261 (1.1)
SVCP	Silver Carp	<i>Hypophthalmichthys molitrix</i>	0	50 (0.2)
SVMW	Mississippi Silvery Minnow	<i>Hybognathus nuchalis</i>	32 (0.1)*	152 (0.6)
TFSD	Threadfin Shad	<i>Dorosoma petenense</i>	306 (1.1)	585 (2.4)
TLSN	Taillight Shiner	<i>Notropis maculatus</i>	365 (1.3)	175 (0.7)
TPMT	Tadpole Madtom	<i>Noturus gyrinus</i>	0	7 (<0.1)
WDSN	Weed Shiner	<i>Notropis texanus</i>	4,348 (16.0)	8,506 (34.3)
WRMH	Warmouth	<i>Lepomis gulosus</i>	517 (1.9)	287 (1.2)
WTBS	White Bass	<i>Morone chrysops</i>	44 (0.2)	6 (<0.1)
WTCP	White Crappie	<i>Pomoxis annularis</i>	329 (1.2)	106 (0.4)
YLBH	Yellow Bullhead	<i>Ameiurus natalis</i>	11 (<0.1)	6 (<0.1)
YWBS	Yellow Bass	<i>Morone mississippiensis</i>	213 (0.8)	9 (<0.1)
		Total number =	26,348	24,786

Fish codes are standard four-letter designations used in this study. Common names and scientific names follow Robison and Buchanan (2020)

* An estimated 14,868 of this species collected from one fyke net in one lake was considered an aberrant catch and excluded from all analyses

the pre-carp period (Table 2). In 2017, longear sunfish (*Lepomis megalotis*) was collected by electrofishing in all 15 lakes ($n=2479$, 23% of the catch), and was the most abundant lepidomid in oxbow lake assemblages overall. Although still collected in 14 of 15 lakes, longear sunfish was only about one-sixth as abundant ($n=269$, 4% of the catch) during the pre-carp period. Other species that exhibited noticeable increases in abundance during the post-carp period included weed shiner (*N. texanus*) ($n=2$, <1 in 2002; $n=441$, 4% in 2017), bigmouth buffalo (*Ictiobus cyprinellus*) ($n=51$, 1% in 2002; $n=220$, 2% in 2017), and smallmouth buffalo (*I. bubalus*) ($n=169$, 2% in 2002; $n=444$, 4% in 2017). Boat electrofishing also captured the vast majority (96%) of bigheaded carps collected during 2017 sampling.

Bluegill (*L. macrochirus*) was among the most common species in lower White River oxbow lakes, having

been collected in all lakes by electrofishing during both the pre-carp and post-carp periods. However, by 2017, longear sunfish had become the most abundant lepidomid in oxbow lake assemblages, with bluegill decreasing from 32% of the overall catch during the pre-carp period ($n=2407$) to 16% during the post-carp period ($n=1739$). Similarly, gizzard shad (*Dorosoma cepedianum*) ($n=1292$) was the second most abundant species from electrofishing during the pre-carp period (17%); however, only 561 (5%) were captured during the post-carp period (fourth most abundant). Other species that exhibited noticeable decreases in abundance between the pre-carp and post-carp periods included orangespotted sunfish (*L. humilis*) ($n=476$, 6% in 2002; $n=355$, 3% in 2017), white crappie (*Pomoxis annularis*) ($n=312$, 4% in 2002; $n=69$, 1% in 2017), and black crappie (*P. nigromaculatus*) ($n=76$, 1% in 2002; $n=36$, <1% in 2017). No

Table 2 Comparison of numbers collected (*N*) and species richness (*S*) between pre-carp (2002) and post-carp (2017) periods in lower White River oxbow lakes

	2002 (Pre-carp)	2017 (Post-carp)
<i>All gears pooled:</i>		
<i>N</i>	26,348	24,786
<i>S</i>	61	67
<i>By gear:</i>		
Electrofishing		
<i>N</i>	7500	10,672
<i>S</i>	46	58
Mini-Fyke Nets		
<i>N</i>	18,446	13,627
<i>S</i>	42	48
Experimental Gill Nets		
<i>N</i>	402	488
<i>S</i>	23	28

These bulk figures include silver carp

other species exhibited notable abundance changes from electrofishing sampling between the pre-carp and post-carp periods.

Mini-fyke nets captured 13,627 fishes that included 48 species during the post-carp period compared to 18,446 fishes containing 42 species during the pre-carp period (Table 2). Weed shiners more than doubled in relative abundance between the pre-carp ($n=4346$; 24% of the catch) and post-carp ($n=8065$; 59% of the catch) periods. Similarly, mimic shiner (*N. volucellus*) ($n=1295$, 7% in 2002; $n=1418$, 10% in 2017) and pallid shiners (*Hybopsis amnis*) ($n=27$, <1% in 2002; $n=289$, 2% in 2017) exhibited smaller abundance increases. Conversely, emerald shiner (*Notropis atherinoides*) ($n=5,844$, 32%) were much more abundant during the pre-carp period compared to the post-carp period ($n=1418$, 10%). Pugnose minnow (*Opsopoeodus emiliae*) ($n=3238$, 17% in 2002; $n=226$, 2% in 2017) and brook silverside (*Labidesthes sicculus*) ($n=1692$, 9% in 2002; $n=227$, 2% in 2017) also exhibited large decreases in abundance between pre-carp and post-carp periods. No other species exhibited notable abundance changes in mini-fyke nets between the pre-carp and post-carp periods. No adult or juvenile bigheaded carps were ever captured using mini-fyke nets during either sampling period.

Experimental gill nets captured a single silver carp during the pre-carp period, though that collection occurred in a lake not used in the current study (East Moon Lake). During the post-carp period, only two bigheaded carp specimens were collected. It was likely that net meshes were too small to effectively sample bigheaded carps, which also tend to be more net shy

than other species (Conover et al. 2007; Chapman and Hoff 2011). Compared to the other to gears, experimental small-mesh gill nets caught the fewest numbers and species of fishes from lower White River oxbow lakes. A total of 488 fishes comprising 28 species were collected from 45 net-sets during the post-carp period, which was comparable to the pre-carp period when 45 net-sets yielded 402 fishes and 23 species (Table 2). However, several species exhibited notable increases in abundance between the pre-carp and post-carp periods. In particular, the three common gars (longnose gar [*Lepisosteus osseus*], shortnose gar [*L. platostomus*], and spotted gar [*L. oculatus*]) all increased in abundance between the pre-carp ($n=48$, 12% of the catch) and post-carp ($n=200$, 41% of the catch) periods. Smallmouth buffalo ($n=17$, 4% in 2002; $n=72$, 15% in 2017), and to lesser extents, freshwater drum (*Aplodinotus grunniens*) ($n=9$, 2% in 2002; $n=44$, 9% in 2017), bigmouth buffalo ($n=4$, 1% in 2002; $n=31$, 6% in 2017), and black buffalo (*I. niger*) ($n=9$, 2% in 2002; $n=25$, 5% in 2017) also exhibited increases during the post-carp period. In fact, these seven species combined constituted 76% of all fishes collected from small-mesh gill nets during the post-carp period compared to only 22% during the pre-carp period. Conversely, gizzard shad ($n=224$, 56%), which represented more than half of the catch during the pre-carp period, comprised only 10% ($n=48$) of the catch during the post-carp period. This finding was consistent with the electrofishing results for this species.

Fish assemblage measures

Two-sample *t*-tests assuming unequal variances were conducted for all fish assemblage measures assessing differences between the pre-carp and post-carp periods. When gear types were pooled and averaged across lakes, *H'*, *D*, and *E* measures were similar between the pre-carp and post-carp periods ($P=0.268-0.859$) (Table 3). However, *S* and H'_{\max} measures were significantly greater during the post-carp period ($P=0.015-0.016$) (Table 3). When tested by individual gear, significant differences existed for all measures based on electrofishing data, with all assemblage measures greater during the post-carp period ($P\leq 0.001-0.032$) (Table 3). Conversely, none of the fish assemblage measures varied between periods with mini-fyke nets ($P=0.153-0.977$) (Table 3). Experimental small-mesh gill net data were intermediate, with some measures differing between periods. Specifically, *H'*, *S*, and related measures *E* and *D* were greater during the post-carp period ($P\leq 0.001-0.049$), with one other measure (H'_{\max}) exhibiting a nearly significant increase ($P=0.054$) (Table 3).

Table 3 T-test comparisons of species richness (*S*), Shannon-Wiener diversity (H' max), species evenness (*E*), standardized species richness (*M*), and Simpson's dominance (*D*) index values between pre-carp (2002) and post-carp (2017) periods in lower White River oxbow lakes

Assemblage variables	2002 (Pre-carp) Mean (± SE)	2017 (Post-carp) Mean (± SE)	<i>P</i>
<i>Gears pooled and averaged across lakes:</i>			
<i>H'</i>	2.25±0.17	2.43±0.15	0.295
<i>H'</i> _{max}	3.61±0.23	3.70±0.03	0.016
<i>E</i>	0.62±0.05	0.66±0.04	0.480
<i>S</i>	37±2	41±1	0.015
<i>M</i>	0.98±0.09	1.08±0.05	0.268
<i>D</i>	0.80±0.06	0.81±0.04	0.859
<i>By gear averaged across lakes</i>			
<i>Electrofishing</i>			
<i>H'</i>	2.29±0.06	2.64±0.04	<0.001
<i>H'</i> _{max}	3.26±0.03	3.48±0.04	<0.001
<i>E</i>	0.70±0.02	0.76±0.01	0.032
<i>S</i>	26±1	33±1	<0.001
<i>M</i>	0.85±0.03	1.34±0.07	<0.001
<i>D</i>	0.82±0.02	0.88±0.01	0.007
<i>Mini-Fyke Nets</i>			
<i>H'</i>	1.53±0.11	1.56±0.14	0.892
<i>H'</i> _{max}	2.91±0.05	2.95±0.09	0.734
<i>E</i>	0.53±0.04	0.53±0.05	0.977
<i>S</i>	19±1	20±2	0.485
<i>M</i>	0.71±0.09	0.89±0.08	0.153
<i>D</i>	0.65±0.05	0.63±0.05	0.705
<i>Experimental Gill Nets</i>			
<i>H'</i>	1.46±0.07	1.93±0.06	<0.001
<i>H'</i> _{max}	2.05±0.05	2.23±0.07	0.054
<i>E</i>	0.71±0.03	0.86±0.01	0.005
<i>S</i>	8±1	10±1	0.049
<i>M</i>	1.61±0.09	1.77±0.11	0.568
<i>D</i>	0.64±0.03	0.81±0.01	<0.001

Bold type signifies difference significant at alpha level of 0.05. Silver carp were not included in these analyses

Fish assemblage structure

As reflected by electrofishing, NMS analyses of pre-carp and post-carp assemblages (final stress for three-dimensional solution=9.46, axes 1–3 explained 90% of variance) differed in multivariate space, with little overlap in assemblage structures. There was strong separation of pre-carp and post-carp assemblages along axis 1, with only slight separation along axis 2 (Fig. 2). In addition, there was a distinct separation in assemblages along axis 3 (not shown). MRPP group testing indicated the structural difference between pre-carp and post-carp

assemblages was highly significant ($P<0.001$). It was suspected that structural differences may have been, at least in part, in response to increasing abundances of big-headed carps occurring at the same time.

The fish assemblage shift detected with electrofishing data was driven by increasing and decreasing abundances of several species between periods, as evidenced by stronger species-axis correlations with NMS axes (i.e., >0.4 or <- 0.4). Electrofishing data suggested increased abundances of longear sunfish, two black basses (*Micropterus* spp.), three buffalofishes (*Ictiobus* spp.), and to a lesser extent, redspotted sunfish (*L. punctatus*) occurred during the post-carp period (Fig. 2). All these species contained either strong negative species-axis 1 correlations, strong positive species-axis 2 correlations, or both. Conversely, electrofishing data also suggested abundance decreases during the post-carp period occurred with bluegill, gizzard shad, white crappie, and to lesser extents, orangespotted sunfish and yellow bass (Fig. 2). These species contained either strong positive species-axis 1 correlations, strong negative species-axis 2 correlations, or both.

With mini-fyke nets (final stress for two-dimensional solution=13.89, axes 1–2 explained 78% of variance), pre-carp and post-carp assemblages still differed significantly in multivariate space (MRPP: $P=0.001$). However, there was much more overlap in assemblage structures compared to electrofishing (Fig. 3). There was little separation of pre-carp and post-carp assemblages along axis 1, though there was moderate separation along axis 2 (Fig. 3). Assemblage differences appeared driven by increased abundances of weed shiner, pallid shiner, and mimic shiner in concert with decreased abundances of orangespotted sunfish, emerald shiner, and pugnose minnow during the post-carp period (Fig. 3). Because the separation of assemblages in multivariate space was not as a distinct with mini-fyke nets compared to electrofishing, species-axis correlations for individual species were generally weaker overall.

With experimental small-mesh gill nets (final stress for two-dimensional solution=16.37, axes 1–2 explained 77% of variance), pre-carp and post-carp assemblages differed significantly in multivariate space (MRPP: $P<0.0001$), with little assemblage overlap as observed with electrofishing (Fig. 4). In general, there was strong separation of pre-carp and post-carp assemblages along axis 1 and no separation along axis 2 (Fig. 4). The shift in fish assemblages was related to several species, most of which were larger-bodied, limnetic-zone species. Assemblage differences appeared to be driven by increased abundances of three buffalofishes, three gars (*Lepisosteus* spp.), and to a lesser extent, freshwater drum during the post-carp period (Fig. 4). All these species contained

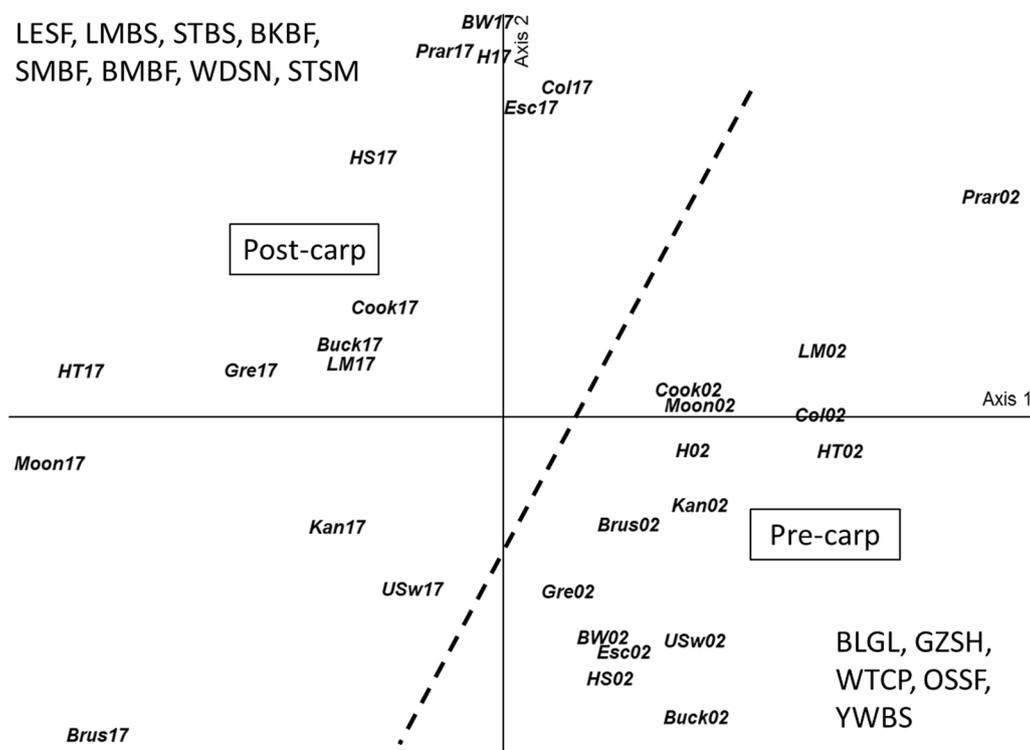


Fig. 2 Nonmetric multidimensional scaling (NMS) lake ordination plots for electrofishing data from 15 oxbow lakes in the lower White River, Arkansas. Dashed line separates pre-carp (right along axis 1 with '02' in label) and post-carp (left along axis 1 with '17' in label) samples. The species shown are those with species-axis correlations either >0.4 or < -0.4 on NMS axis 1 and/or 2. Four-letter species codes are located in Table 1. Silver carp were not included in these analyses

strong positive species-axis 1 correlations, strong species-axis 2 correlations (positive and negative), or both. Conversely, assemblage differences also were driven by abundance decreases observed with gizzard shad, and to lesser extents, yellow bass and skipjack herring (*Alosa chrysochloris*) during the post-carp period (Fig. 4). These species contained strong negative species-axis 1 correlations, strong species-axis 2 correlations (positive and negative), or both.

Discussion

Assemblage effects

The probable effects of bigheaded carp establishment on native oxbow lake fish assemblages in the lower White River were collectively mixed and sometimes gear-specific. It was apparent that carp effects on assemblages were more difficult to assess using traditional assemblage measures such as *S*, *H'*, *E*, and *D*. Although mean *S* across lakes increased significantly during the post-carp period with electrofishing, gill nets, and when all gears were pooled, some of the increases were related to two additional invasive carp species being collected in 2017 that were not collected in 2002 (grass carp [*Ctenopharyngodon idella*], and black carp [*Mylopharyngodon*

piceus]; refer to Table 1). Mean *H'* and *E* across lakes also increased significantly during the post-carp period, but only with electrofishing and gill nets. Interestingly, although *E* increases were small, they suggested that individual species' compositions had become proportionally more uniform across lake assemblages during the post-carp period, at least with two of the gears used. This observation would be consistent with oxbow lake fish assemblages becoming more "homogenized" following the establishment of an invasive species, which has been documented previously (e.g., Rahel 2000; Olden and Poff 2004). Additionally, the more than three-fold increase in abundance of gill net fish assemblages by seven common riverine species (i.e., longnose, shortnose, and spotted gars; smallmouth, bigmouth, and black buffaloes; and freshwater drum) during the post-carp period also would be consistent with oxbow lake fish assemblages becoming homogenized.

Multivariate techniques demonstrated other aspects of fish assemblage shifts more clearly, which were related to both small and large changes in abundances of more than 20 species (Table 4). Although these periods were separated temporally by 15 years, we presumed our observations were, in part, directly or indirectly associated with

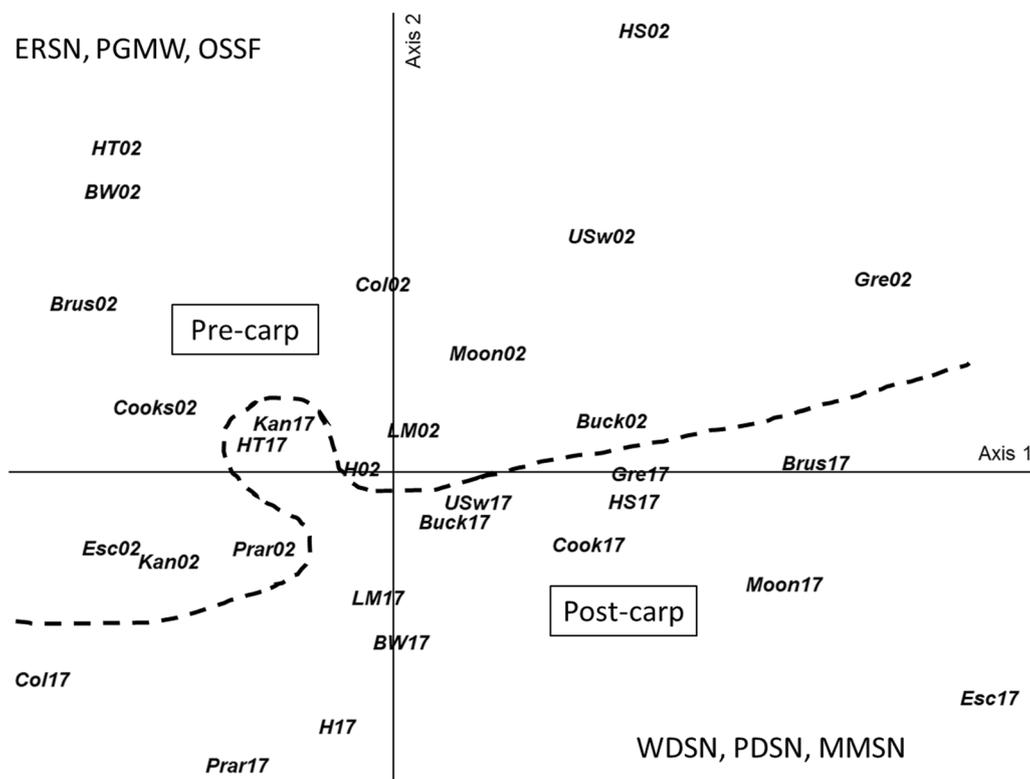


Fig. 3 Nonmetric multidimensional scaling (NMS) lake ordination plots for mini-fyke net data from 15 oxbow lakes in the lower White River, Arkansas. Dashed line separates pre-carp (upper and left with '02' in label) and post-carp (lower and right with '17' in label) samples. The species shown are those with species-axis correlations either >0.3 or <-0.3 on NMS axis 1 and/or 2. Four-letter species codes are located in Table 1. Mini-fyke net fish assemblages exhibited significant overlap in multivariate space

bigheaded carp establishment. In a similar study from the Illinois River, Solomon et al. (2016) reported that the greatest dissimilarity between their pre-carp and post-carp fish assemblages was related to 26 different species. Previous studies (e.g., Irons et al. 2007; Solomon et al. 2016; Pendleton et al. 2017; Phelps et al. 2017) have suggested inverse relationships between bigheaded carps and catostomids, especially bigmouth buffalo, which is a planktivore native to the Mississippi River basin. Conversely, we observed increases in the abundances of all three common buffalofish species (bigmouth, smallmouth, and black) during the post-carp period. Thus, competition or other negative interactions between bigheaded carps and buffalofishes suggested from previous studies were either not occurring in lower White River oxbow lakes or had not developed because their common resource was not yet limited (e.g., Sampson et al. 2009). Alternatively, from experimental pond studies using bighead carp presence as treatments, Collins and Wahl (2017) suggested the possibility that excessive carp feeding in the limnetic zone generated a spillover effect to the benthic zone (e.g., Yallaly et al. 2015). This effect potentially increased the biomasses of Chironomidae

larvae, which are common food sources for all three buffalofishes. This possibility in lower White River oxbow lakes might explain our observations with buffalofishes, and perhaps also freshwater drum. Three common gar species (longnose, shortnose, and spotted) also were more abundant in lower White River oxbow lakes during the post-carp period. Solomon et al. (2016) reported that all three gars were positively associated with bigheaded carps in their study and suggested that bigheaded carp-induced declines by other species might have freed up food resources for gars, which lead to their increased abundances. The same carp-gar scenario could be occurring in lower White River oxbow lakes.

The lack of any fish assemblage differences with mini-fyke nets between the pre-carp and post-carp periods was not surprising given that mini-fyke nets target more small-bodied species (e.g., *Notropis* spp. and juveniles of many species) in the portion of the littoral zone that was less than one meter deep. Thus, fewer assemblage differences might be expected given that bigheaded carp effects have been more commonly documented for larger-bodied, offshore species (e.g., Irons et al. 2007; Solomon et al. 2016; Pendleton et al. 2017; DeBoer et al.

Pendleton et al. 2017; Fritts et al. 2018; Fletcher et al. 2019; Chick et al. 2020) are probably also occurring in lower White River oxbow lakes following bigheaded carp establishment.

Individual species effects

Several lower White River oxbow lake species exhibiting the greatest decreases in abundance between the pre-carp and post-carp periods should be of concern to fisheries and WRNWR managers. White crappie, and to a lesser extent black crappie, are two of the most important sport fisheries in the lower White River and the WRNWR, with most of the fishery existing in oxbow lakes and other floodplain habitats (J. Homan, AGFC, personal communication). Both crappies were largely collected from electrofishing sampling, with white crappie being about 3–4 fold more abundant on average than black crappie. Crappies are cyclic species that are well-documented to exhibit highly variable recruitment, with one exceptionally strong year-class dominating the fishery for several years (Allen and Miranda 1998, 2001). In this study, white crappie was one-fifth as abundant and black crappie half as abundant during the post-carp compared to the pre-carp period. Although it cannot be ruled out that crappies may have simply been in a down cycle during 2017 and there was no actual link with bigheaded carps, there is anecdotal evidence from anglers who believe that several years of declining crappie fisheries have coincided with large carp populations now being well established in the WRNWR (A. Hitchcock, USFWS, personal communication). Given the popularity of the crappie fisheries and the lack of other studies reporting crappie declines in response to carps, more in depth studies are needed to determine through what pathways (e.g., competition for food, ichthyoplankton predation, disrupted spawning, increased turbidity, etc.) bigheaded carps might be affecting crappies in this region.

Gizzard shad is a very common species in the lower White River, and as such, are important components of oxbow lake food webs. Gizzard shad are important prey for many species, including many sportfishes, and are often important components of many aquatic food webs. Other studies have documented declines in gizzard shad catches and condition following establishment by bigheaded carps (Irons et al. 2007; Pendleton et al. 2017; Pyron et al. 2017; Fritts et al. 2018). In this study, gizzard shad exhibited noticeable declines in abundance during the post-carp period as reflected by all three gears. In addition, mean relative weights of gizzard shad were only $78 \pm SE$ of 1 during the post-carp period (unpublished data), though no comparable data were available from the pre-carp period. Pyron et al. (2017) also reported crashes of gizzard shad populations in an Ohio River sub-basin

(Wabash River) following the bigheaded carp establishment in the 1990s. However, following stable isotope analyses on resident food webs, they concluded that, although bigheaded carps may have indirectly influenced the gizzard shad population crash, there were multiple other stressors that also likely contributed. Factors that operated at decadal scales such as increased urbanization, agricultural nutrient loading, instream habitat alterations, and hydrologic variability all likely played roles in the gizzard shad decline. Furthermore, Pyron et al. (2017) characterized the Ohio-Wabash river bigheaded carp invasion as an “opportunistic” invasion rather than a “hostile takeover” invasion. Gizzard shad declines also have been observed following bigheaded carp establishment in oxbow lakes of the lower Mississippi River and some of its sub-basins in Mississippi (e.g., Yazoo River) during the 2000s (L. Pugh, Mississippi Department of Wildlife Fisheries and Parks, personal communication). Despite that other factors may have played roles in gizzard shad declines, studies have collectively suggested that high diet overlap between bigheaded carps and gizzard shad as a major causative agent that at least, in part, have affected the declines (Irons et al. 2007; Sampson et al. 2009; Phelps et al. 2017; Minder and Pyron 2017; Pyron et al. 2017). It is plausible that the same carp-shad interactions purported in the upper Mississippi River basin also are occurring in lower White River oxbow lakes.

Bluegill also is a very common species in the lower White River, and as such, are also important components of oxbow lake food webs. Although not as popular as crappies, they also are a moderately important sportfish. However, the mechanism of why bluegill might be impacted by bigheaded carps is not entirely clear. Between the pre-carp and post-carp periods, bluegill abundances declined by about 30% on average as reflected by electrofishing, which also was mirrored by a decrease in the overall abundance of other insectivores. The bluegill decline occurred coincident with abundance decreases of congeners such as orangespotted sunfish and increases of others like longear sunfish, and to a lesser extent, redspotted sunfish. From experimental pond studies, Collins et al. (2017b) suggested that bighead carp may enhance growth and survival of juvenile bluegill through indirect food-web mechanisms whereby bluegill consumed more cladocerans and macroinvertebrates in the presence of carps. In that study, it was hypothesized that carp-induced cladoceran migrations away from the limnetic zone occurred that made them more available to juvenile bluegills in littoral-zone vegetation. Previous studies have not widely reported possible carp effects on bluegill in the wild or on the other species above. Nonetheless, previous studies have concluded that

bigheaded carps can disrupt aquatic food webs through a variety of direct and indirect pathways, and that future studies were needed to elucidate these effects (DeBoer et al. 2018; Ochs et al. 2019). This general conclusion was supported by other studies emphasizing different species (e.g., Pendleton et al. 2017; Pyron et al. 2017; Fritts et al. 2018). Given the importance of bluegills in many aquatic food webs in the southern USA, further research is needed to elucidate pathways and mechanisms for possible carp effects.

Few other studies have reported many findings with small-bodied cyprinids within the context of bigheaded carp effects. Between the pre-carp and post-carp period, we observed large decreases in the abundances of emerald shiner and pugnose minnow (both insectivores) coincident with large increases in the abundance of weed shiner (an omnivore). To lesser extents, mimic shiner and pallid shiner (both insectivores) also increased and brook silverside (an insectivore) decreased during the same period. Hayer et al. (2014) also reported declines in emerald shiner in South Dakota waters following invasion by bighead carp. They suggested that emerald shiners and silver carp competed for zooplankton, and that shiners may have moved to more benthic habitats to avoid competition with carps. Conversely, Solomon et al. (2016) indicated a positive association between bigheaded carps and emerald shiners in the Illinois River. To our knowledge, no other studies have mentioned possible effects on the other species above, though the mechanisms proposed for emerald shiner would be applicable to these species as well. Future studies may need to assess several small-bodied cyprinids for possible carp effects.

Species lost and gained

Post-carp period oxbow lake fish assemblages in the lower White River did exhibit some differences compared to the pre-carp period. However, there was no evidence to date suggesting that carp establishment had extirpated any species within native assemblages. Although there may have been instances of local extirpations in a given lake (or lakes), all species recorded as “lost” or “gained” between the pre-carp and post-carp periods were historically rare and less than 0.2% of the overall assemblage (Table 5). Of the 11 species gained following carp establishment, four species (silver carp, bighead carp, grass carp, and black carp) were invasive carps themselves (Table 5). Of the species classified as lost, most were small-bodied species that were likely present but not collected due to random variation associated with sampling. Given the numbers collected during the pre-carp period, dollar sunfish (*L. marginatus*) not being collected during the post-carp period was surprising (Table 5). However, the species is at the edge of its distribution in the lower

Table 5 Fish species unique to pre-carp (2002) and post-carp (2017) sampling in lower White River oxbow lakes

Species present only during pre-carp period (2002)	N	Species present only during post-carp period (2017)	N
Chestnut Lamprey	1	Alligator Gar	2
Dollar Sunfish	57	Bighead Carp*	1
Golden Topminnow	1	Bullhead Minnow	42
Grass Pickerel	1	Black Carp*	1
Highfin Carpsucker	1	Bluntnose Minnow	2
Lake Chubsucker	4	Cypress Darter	51
Northern Starhead Topminnow	5	Flier	1
Sauger	7	Goldeye	5
		Grass Carp*	6
		River Darter	2
		Silver Carp*	50

No species listed comprised more than 0.2% of the total catch. N=number collected across all gears

*Invasive carp species

White River and small specimens in the field can be confused with small longear sunfish (Robison and Buchanan 2020). As for the cypress darter (*Etheostoma proeliare*) and bullhead minnow (*Pimephales vigilax*), both species were caught in low abundances during the post-carp period after having not been collected during the pre-carp period. However, their post-carp catches were widespread with cypress darter being captured in 12 of 15 lakes and bullhead minnow in 7 of 15 lakes. Given that these species were small-bodied with average sizes of about 30–60 mm, it was probable these species present during the pre-carp period, though missed entirely during sampling or perhaps misidentified.

Alternative explanations to observations

Although confirmed that bigheaded carps had established in the lower White River sometime between 2002 and 2017, we acknowledge that fish assemblage shifts or other effects detected from this study can never be linked exclusively to bigheaded carps. Although environmental conditions in the lower White River were relatively similar between the pre-carp and post-carp periods, some potentially important differences did exist. For example, mean daily river stage at the Clarendon, Arkansas gage (just upstream of the study lakes) was 0.8 m greater on average prior to the post-carp sampling period compared to years preceding the pre-carp period (Table 6). In fact, increased stages in the years prior to the post-carp sampling could have facilitated bigheaded carp establishment in these particular oxbow lakes. Stages were equally variable between the two periods, however, this degree of hydrologic increase as it might influence river-lake

Table 6 Comparison of environmental conditions in lower White River oxbow lakes during pre-carp (2002) and post-carp (2017) sampling periods

Parameter	Pre-carp period (2002) (mean ± SE)	Post-carp period (2017) (mean ± SE)
<i>Lake morphometric</i>		
Surface area (ha)	20.8 ± 2.5	24.6 ± 3.3
Length–width ratio	16.6 ± 1.6	19.0 ± 2.6
Mean depth (m)	2.2 ± 0.2	2.6 ± 0.3
<i>Water quality</i>		
Secchi (cm)	65 ± 4	53 ± 3
Temperature (°C)	23.6 ± 1.1	24.9 ± 0.3
Dissolved oxygen (mg/L)	7.6 ± 0.4	6.6 ± 0.1
Conductivity (µS/cm)	230 ± 5	262 ± 8
Total dissolved solids (mg/L)	130 ± 3	170 ± 5
Morpho-edaphic index (%)	72.4 ± 6.2	75.9 ± 7.7
<i>Hydrology</i>		
Mean daily stage – preceding years (m)	5.1 ± 1.6*	5.9 ± 1.7**
Daily stage CV (%)	30.7	28.9

* Mean calculated for 1980–1984 and 1996–2002 for 2002 sampling (gage inoperable during intervening years)

** Mean calculated for 2003–2016 for 2017 sampling

connectance is unknown and could not be assessed from this study. Other smaller differences with respect to water quality, temperature, and lake morphometry were not expected to have been great enough affect oxbow lake fish assemblages.

Although this study was multiple-gear and very comprehensive, it was limited to only 2 years of data collection 15 years apart. As a result, we cannot thoroughly assess the degree of interannual variability that occurs naturally within these particular oxbow lake fish assemblages. Although regular long-term monitoring data does not exist for any of these lakes or location in the lower White River basin, we are able to examine this variation. In these particular oxbow lakes, Clark (2006) compiled data from five of our study lakes sampled over three different years (2002 [this study], 2004, and 2005). Using the relative abundances from all gears pooled, mean coefficients of variation were 61% for six large-bodied species (largemouth bass [*Micropterus nigricans*], common carp [*Cyprinus carpio*], spotted gar, gizzard shad, and white crappie), 52% for four lepidomid species (bluegill, longear sunfish, orangespotted sunfish, and warmouth [*Lepomis gulosus*]), and 93% for three cyprinid species (emerald shiner, weed shiner, and pugnose minnow). These same figures computed for pre-carp (2002) and post-carp (2017) sampling done in this study were all lower, equaling 41%, 39%, and 74%, respectively. Thus, the interannual variation observed in oxbow lake fish assemblages over 15 years appeared comparable (though lower) to variation observed over shorter periods of time,

including consecutive years. Although we do not consider this evidence beyond question, previous studies assessing the degree of interannual variability in riverine fish assemblages are collectively mixed. Moderate to high annual variability has been documented with riverine fish assemblages previously (e.g., Broadway et al. 2015; Shields et al. 2021), though some studies (e.g., Murry and Farrell 2014) have documented fish river assemblages to remain relatively stable through time. This finding was especially true with respect to their core species, as was generally observed in this study.

Future expansion by bigheaded carps

The upstream reaches of the White River, Arkansas above the WRNWR are easily susceptible to further range extensions by bigheaded carps. This reach includes Bayou DeView as well as the Cache and Black rivers and their tributaries. However, range extensions further up into the White River basin above Batesville, Arkansas will not be as likely due the presence of several large dams with cold-water releases. Niche models have indicated that most riverine habitats in the Mississippi River basin are suitable for the completion of bigheaded carp life cycles (O'Connell et al. 2011). While the modeling scenarios outlined by O'Connell et al. (2011) assume that all Mississippi River segments were equal regarding reproductive habitat and invasion potential, it is unclear how well this model applies to serial lock-and-dam systems like the McClellan-Kerr Arkansas River Navigation System (MKARNS), which

is adjacent to the lower White River and connected to the White River by the Arkansas Post Canal. Although bigheaded carps have been documented in the MKARNS as far upstream as Dardanelle Dam in Russellville, Arkansas, they have presently not been documented further upstream. However, abnormal flooding in the Arkansas River (e.g., in 2019) could, at any time, result in rapid, explosive increases in bigheaded carp abundances upstream as has been observed elsewhere (e.g., Barko et al. 2006; DeGrandchamp et al. 2008; Lohmeyer and Garvey 2009; Pyron et al. 2017). This idea is consistent with Havel et al. (2005), who suggested that reservoir systems (regardless of type) may facilitate the spread of invasive species, in effect, acting as stepping stones for the species into a new river basin. Assuming this is at least partly true, the Arkansas River and its MKARNS waterway could be ideal for rapid invasion by bigheaded carps upstream towards Oklahoma and Kansas. Impacts of further range expansions by bigheaded carps in Arkansas are unclear, though this study suggests that wide establishment could induce detectable changes on native fish assemblages.

Acknowledgements

This research was funded in part by the U.S. Fish and Wildlife Service—Gulf States Marine Fisheries Commission through the Gulf & Atlantic Regional Panel on Aquatic Invasive Species, and the U.S. Fish and Wildlife Service—Lower Mississippi River Conservation Committee. Additional financial support and facilities were provided by the Aquaculture/Fisheries Center at the University of Arkansas at Pine Bluff (UAPB). We also thank the many UAPB students and staff who assisted with fish sampling. We express great appreciation for lodging and the extensive assistance from multiple personnel at the U.S. Fish and Wildlife Service—Dale Bumpers White River National Wildlife Refuge in Clarendon, Arkansas.

Author contributions

ME designed the study. CS, JK, SS, and ME collected and analyzed the data. ME wrote the original manuscript, with all authors contributing towards finalizing the manuscript.

Funding

U.S. Fish and Wildlife Service—Gulf States Marine Fisheries Commission through the Gulf & Atlantic Regional Panel on Aquatic Invasive Species and the U.S. Fish and Wildlife Service—Lower Mississippi River Conservation Committee. Additional financial support and facilities were provided by the Aquaculture/Fisheries Center at the University of Arkansas at Pine Bluff (UAPB).

Availability of data and materials

All data are available Aquaculture/Fisheries Center at the University of Arkansas at Pine Bluff (UAPB).

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Received: 5 July 2023 Accepted: 10 February 2024

Published online: 27 February 2024

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