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Identification of Bighead Carp and Silver Carp early-life environments and inferring Lock and Dam 19 passage in the Upper Mississippi River: insights from otolith chemistry

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Abstract

Knowledge of environments used during early life history and movement patterns of Bighead Carp (*Hypophthalmichthys nobilis*) and Silver Carp (*H. molitrix*), collectively termed bigheaded carps, in the Upper Mississippi River (UMR) would be valuable for informing control measures to limit further population expansion and impacts of these species. Lock and Dam 19 (LD19) is a high-head dam on the UMR that delineates downriver areas where bigheaded carps are well established from upriver pools where these species are less abundant and evidence of reproduction and recruitment are limited. Principal natal environments supporting recruitment of emerging bigheaded carp populations in the UMR are unknown. The objectives of this study were to (1) infer environments occupied during early-life stages by bigheaded carps collected in UMR Pools 19–21 during 2013–2014 using otolith microchemistry and stable isotope analyses, and (2) use early-life environment assignments and capture location to identify individuals that passed through LD19. Differences in multivariate water chemistry signatures (Sr:Ca, Ba:Ca and δ18O) among the UMR, its tributaries, and the Missouri and Middle Mississippi rivers enabled development of a classification model for inferring early-life environment of bigheaded carps. Multiple sources of recruits, including from tributaries, have contributed to upriver expansion of bigheaded carps in the UMR. Sustainable control of bigheaded carps upstream of LD19 will likely require efforts to control local recruitment and immigration from downriver. The frequency of bigheaded carps collected in Pool 19 that were downstream of LD19 during early life suggests that bigheaded carps upstream of LD19 still predominantly consisted of immigrants from downriver during 2013–2014. Otolith chemistry provides an approach for assessing the extent to which changes in abundance of bigheaded carps upstream of LD19 are associated with local recruitment or immigration from downriver.

Keywords

Asian Carp, Hypophthalmichthys, Stable isotopes, Microchemistry, d18O, Sr:Ca, Ba:Ca

Disciplines

Ecology and Evolutionary Biology | Natural Resources Management and Policy | Terrestrial and Aquatic Ecology

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ORIGINAL PAPER

Identification of Bighead Carp and Silver Carp early-life environments and inferring Lock and Dam 19 passage in the Upper Mississippi River: insights from otolith chemistry

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Abstract Knowledge of environments used during early life history and movement patterns of Bighead Carp (*Hypophthalmichthys nobilis*) and Silver Carp (*H. molitrix*), collectively termed bigheaded carps, in the Upper Mississippi River (UMR) would be valuable for informing control measures to limit further population expansion and impacts of these species. Lock and Dam 19 (LD19) is a high-head dam on the UMR that delineates downriver areas where bigheaded carps are well established from upriver pools where these species are less abundant and evidence of reproduction and recruitment are limited. Principal natal environments supporting recruitment of emerging bigheaded carp populations in the UMR are unknown. The objectives of this study were to (1) infer environments occupied during early-life stages by bigheaded carps collected in UMR Pools 19–21 during 2013–2014 using otolith microchemistry and stable isotope analyses, and (2) use early-life environment assignments and capture location to identify individuals that passed through LD19. Differences in multivariate water chemistry signatures (Sr:Ca, Ba:Ca and $\delta^{18}O$) among the UMR, its tributaries, and the Missouri and Middle Mississippi rivers enabled development of a classification model for inferring early-life environment of bigheaded carps. Multiple sources of recruits, including from tributaries, have contributed to upriver expansion of bigheaded carps in the UMR. Sustainable control of bigheaded carps upstream of LD19 will likely require efforts to control local recruitment and immigration from downriver. The frequency of bigheaded carps collected in Pool 19 that were downstream of LD19 during early life suggests that bigheaded carps upstream of LD19 still predominantly

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consisted of immigrants from downriver during 2013–2014. Otolith chemistry provides an approach for assessing the extent to which changes in abundance of bigheaded carps upstream of LD19 are associated with local recruitment or immigration from downriver.

Keywords Asian Carp · *Hypophthalmichthys* · Stable isotopes · Microchemistry · $\delta^{18}O$ · Sr:Ca · Ba:Ca

Introduction

Bighead Carp (*Hypophthalmichthys nobilis*) and Silver Carp (*H. molitrix*), collectively bigheaded carps, are native to large rivers in eastern Asia and were brought to the United States in the 1970s to improve the water quality in aquaculture ponds (Kolar et al. 2007). By the 1990s, both species had become widely distributed in the lower and middle reaches of the Mississippi River and its tributaries (USGS Nonindigenous Aquatic Species Database; https://nas.er.usgs.gov). The high fecundity and trophic position (planktivores) of bigheaded carps suggest that they compete with nearly all native fishes during their obligate planktivore stages (i.e., post-larvae and fry) (Kolar et al. 2007; Cudmore et al. 2011). Bigheaded carps may also compete for food with native adult planktivores, such as Paddlefish *Polyodon spathula*, Bigmouth Buffalo *Ictiobus cyprinellus*, and Gizzard Shad *Dorosoma cepedianum* (e.g., Schrank et al. 2003; Irons et al. 2007; Sampson et al. 2009). Bigheaded carps have become biomass dominants in some reaches and tributaries of the Mississippi River Basin (Upper Mississippi River Restoration Program Long Term Resource Monitoring data at https://www.umesc.usgs.gov/ltrmp.html; Sass et al. 2010) where they are thought to be affecting plankton resources (Sass et al. 2014) and native fish assemblages (Solomon et al. 2016). Silver Carp also pose a physical threat to boaters because of their large adult size and propensity to jump in excess of a meter above the water when frightened by boat motors (Vetter and Mensinger 2016). These impacts to ecosystem services provided the impetus for national (Conover et al. 2007) and regional plans, including for the Upper Mississippi River (MICRA 2016), to control and contain bigheaded carps and related species.

The reproductive front, defined here as the upstream-most reach where reproduction has been confirmed, in the mainstem Upper Mississippi River (UMR) for both Bighead Carp and Silver Carp is between Lock and Dam (LD) 19 near Keokuk, Iowa and LD15 near Davenport, Iowa (Larson et al. 2017). This 190-km reach has been designated as the UMR bigheaded carp management zone where control and containment measures are being used (i.e., removal by contract fishing) or considered (e.g., deterrents at LD19) to prevent spread upstream (MICRA 2016). Despite reproduction in this reach, the abundance of bigheaded carp upstream of LD19 appears much lower than the abundance downstream of LD19 (Maher 2016; J. Lamer unpublished data).

Bighead Carp and Silver Carp are potamodromous, pelagic broadcast spawners that migrate upstream to spawn in large aggregations (Li et al. 2013). Bigheaded carps spawn multiple times in one season, but generally only after water temperature exceeds 17 °C and discharge is high or rising (Krykhtin and Gorbach 1981; Deters et al. 2013; Li et al. 2013; Larson et al. 2017). Bigheaded carp eggs drift downstream before hatching, then the larvae continue to drift until gas bladder inflation, at which point larvae may move to low-flow nursery areas; survival of eggs that do not remain suspended in the water column is greatly diminished (George and Chapman 2013). The time from spawning to hatch to gas bladder inflation, and thus drift time and distance for eggs and larvae, is inversely related to water temperature (George and Chapman 2013). Depending on flow and temperature, eggs and larvae may continuously drift for 25–100 km (Kolar et al. 2007; Murphy and Jackson 2013), although Grass Carp has spawning and early-life habitat requirements similar to bigheaded carps and can complete larval development to gas bladder inflation having drifted < 25 km (Embke et al. 2018). Due to habitats needed for spawning and early life history, longitudinal and lateral connectivity in rivers likely affects bigheaded carp reproduction, recruitment, and ultimately invasion success.

The UMR between St. Paul, Minnesota and St. Louis Missouri has 29 navigation dams with locks and many floodplain levees that could affect bigheaded carp recruitment. Each navigation pool (e.g., Pool 19) is named for the lock and dam (LD) structure on its downstream end. Of the 29 LD structures, LD1 and LD19 are unusual because they have a much greater hydraulic head than the remaining dams (> 11 m vs 1.8–7.3 m) (Theiling and Nestler 2010). The spillway for LD19 is also unique in having an elevated concrete sill that maintains a vertical drop ($\sim$ 6 m) across the dam even when the spillway lift-gates are completely open (Wilcox et al. 2004). This vertical drop precludes upstream fish passage through the gated portion of LD19, hence the only viable upstream passage for fish is through the lock. By contrast, at high flow other LD structures in the UMR open their gates and allow open river conditions that may enable fish passage through the dam spillway (Theiling and Nestler 2010). Lock and Dam 19 also creates a large impounded area just upstream, which may trap floating eggs and larvae, allowing them to sink. As a result, LD19 may reduce movement and recruitment success of bigheaded carps.

Management actions being implemented or considered are aimed at reducing adults already at the reproductive front upstream of LD19 and preventing more adults from migrating into this reach from downstream (MICRA 2016). This strategy is designed to reduce or eliminate reproduction in the UMR bigheaded carp management zone and minimize fish available to move farther upstream. However, it is not known how important immigration through LD19 is for supporting recruitment of bigheaded carps in the UMR bigheaded carp management zone. Similarly, recruitment sources for bigheaded carps downstream of LD19 are unknown. Better understanding of bigheaded carp recruitment sources in the UMR upstream of LD19, and in the reach immediately below, will help determine if these strategies are capable of achieving management objectives.

Analyses of otolith stable isotope and elemental compositions can provide insights regarding environmental history of individual fish in a variety of environments (Pracheil et al. 2014), including the Mississippi River and tributaries (Zeigler and Whitledge 2011; Laughlin et al. 2016). Otolith composition is strongly correlated with elemental concentrations and stable isotope ratios in the surrounding waters; once formed, otoliths are metabolically inert (Campana and Thorrold 2001). If a fish remains in a location long enough, the surrounding waters impart a permanent chemical signature in the otolith (Pracheil et al. 2014). Otolith chemistry has been used to assess environments used by early-life stages (larval and early-juvenile stages during age-0) for bigheaded carps in the Illinois River (Norman and Whitledge 2015), but has not yet been applied to investigate environments used during early-life stages by bigheaded carps in the UMR. Therefore, our study objectives were to infer environments used during early life (larval and early-juvenile stages during age-0) by invasive bigheaded carps in Pools 19, 20, and 21 of the UMR using otolith chemistry and to identify LD19 passage by individual fish based on early-life environment inferred from otolith chemistry and fish collection location.

Materials and methods

Water sampling and analyses

Water samples were collected monthly during June through September 2006–2016 from the Illinois, Missouri, and Middle Mississippi (section of the Mississippi River between the mouths of the Missouri and Ohio rivers) rivers and the UMR downstream of LD19 (Fig. 1). Water sampling in other potential bigheaded carp natal rivers or river reaches was also conducted during June through September, but began in 2011 (Salt, Des Moines, Iowa, and Cedar rivers; UMR upstream of LD19), 2013 (Rock River), or 2014 (Skunk River). Tributaries that enter the UMR upstream of LD15 were not considered to be potential environments used by early-life stages of bigheaded carps in our study area because there is no evidence of reproduction and adults are rarely reported upstream of Pool 16 (Larson et al. 2017). Bigheaded carps have a protracted spawning season, peaking during mid-May through early July and sometimes extending into August, depending on flow conditions and temperature (Lohmeyer and Garvey 2009; Deters et al. 2013; Larson et al. 2017). Thus, months when water samples were collected were chosen to encompass most of the growing season for age-0 bigheaded carps and the time of year when they are typically present. Two water samples were collected from near the river surface at each location on each collection date and filtered into 20-ml scintillation vials using acid-cleaned polypropylene syringes and 0.45-µm polypropylene syringe filters (Shiller 2003). One sample was used for stable oxygen isotope analysis and the second sample was analyzed for calcium, strontium, and barium concentrations. Vials containing water samples for stable oxygen isotope analysis were filled to the rim

Fig. 1 Map of the central portion of the Mississippi River basin encompassing areas where reproduction by bigheaded carps is known to occur. Rivers that were considered to be potential natal and age-0 nursery environments for bigheaded carps in Pools 19–21 of the Upper Mississippi River are labelled. Upper Mississippi River is upstream of the Missouri River confluence; Middle Mississippi River extends from the Missouri River confluence to the mouth of the Ohio River. Solid lines across the Upper Mississippi River indicate locations of locks and dams. Open circles indicate water sampling locations. Shaded area in inset shows area included in the map

and sealed with Parafilm® to curtail evaporative loss and fractionation (Kendall and Caldwell 1998). Samples were analyzed for stable oxygen isotopic composition using a high-temperature conversion elemental analyzer interfaced with a Thermo Finnigan Delta V® isotope ratio mass spectrometer at the Southern Illinois University Mass Spectrometry Facility. All stable isotope ratios were expressed in standard delta notation, defined as the parts per thousand deviation between the isotope ratio of a sample and standard material (Vienna Standard Mean Ocean Water for water $\delta^{18}O$):

$$\delta^{18}O\ (‰) = [(Rsample/Rstandard) - 1] \times 1000;$$

where R represents $^{18}O/^{16}O$. Analytical precision estimated from analysis of laboratory standards was 0.07‰. Analysis of water samples for calcium, strontium, and barium concentrations was conducted at the Center for Trace Analysis, University of Southern Mississippi. In the laboratory, water samples were acidified to pH 1.8 using ultrapure HCl and allowed to sit acidified for at least 1 week before analysis. Samples were then diluted 11 × in ultrapure 0.16 M HNO_3. The nitric acid contained 2 ppb scandium, indium, and thorium as internal standards. External certified reference standards were also prepared using the same HNO_3 used for sample dilutions. Samples were analyzed for ^{44}Ca ^{88}Sr, and ^{137}Ba in medium resolution using a Thermo-Finnigan Element 2 inductively coupled plasma mass spectrometer (ICPMS). Precision of analyses based on repeated measurements of standards was better than ± 2% (2 SD). Water strontium, barium, and calcium concentration data were converted to molar Sr:Ca and Ba:Ca ratios (mmol/mol).

Fish sampling, otolith preparation and otolith chemistry analyses

Adult Bighead Carp (714–1260 mm total length; n = 46) and Silver Carp (545–967 mm total length; n = 150) were collected from Pools 19, 20, and 21 in the UMR during 2013–2014. Fish were collected using pulsed DC (60 pulses/s) boat electrofishing and monofilament gill nets.

Lapilli otoliths were removed from each fish using non-metallic forceps, rinsed with distilled water to remove adhering tissue, and stored dry in polyethylene microcentrifuge tubes until preparation for stable isotope and elemental analyses. One otolith from each fish was used for stable oxygen isotope analysis. Otoliths were embedded in Epo-fix epoxy (Electron Microscopy Sciences Inc., Hatfield, PA), sectioned in the transverse plane using an ISOMET low-speed saw, sanded using silicon carbide sandpaper (800, and 1000 grit) to achieve a 1-mm section centered on the otolith primordium, and polished with lapping film. Sectioned otoliths were affixed to glass microscope slides using cyanoacrylate glue. A 300-μg subsample of $CaCO_3$ powder was drilled from the core of each otolith (centered on the primordium) using a New Wave Research micromill and placed in a Labco Exetainer vial. Stable oxygen isotope analysis of otolith subsamples was conducted using a ThermoFinnigan Delta V® isotope ratio mass spectrometer interfaced with a Gas Bench II® carbonate analyzer at the Southern Illinois University Mass Spectrometry Facility. All measurements are reported in standard delta notation ($\delta^{18}O$, ‰) relative to the Vienna Pee Dee Belemnite standard. Analytical precision estimated from analysis of laboratory standards was 0.09‰ for $\delta^{18}O$.

The second lapillus from each fish was used for analysis of Sr:Ca and Ba:Ca. Otolith embedding, sectioning, and polishing were as described for stable oxygen isotope analysis, except that the target thickness of the sectioned otolith for analysis of Sr:Ca and Ba:Ca was 0.5 mm. Polished sections were mounted on acid-washed glass microscope slides using double-sided tape, ultrasonically cleaned for 5 min in ultrapure water, dried for 24 h under a class 100 laminar flow hood, and stored in acid-washed polypropylene Petri dishes in a sealed container until analysis. Elemental analysis of otoliths was performed at the Great Lakes Institute for Environmental Research (GLIER), University of Windsor (Windsor, Ontario, Canada). Sectioned otoliths were analyzed for strontium, barium, magnesium, and calcium concentrations using an Agilent 7900 ICPMS coupled with a Teledyne Photon Machines Analyte Excite 193 nm, ultrashort pulse ArF excimer laser. The laser ablated a spot centered on the otolith primordium (25 μm spot size, 600 shots/spot, laser pulse width = 4 nm, 2 mJ/pulse, repetition rate = 20 Hz). Isotopes assayed included ^{43}Ca, ^{88}Sr, ^{138}Ba, and ^{25}Mg. Each sample analysis was preceded by a 60 s gas blank measurement. A standard (NIST 610; National Institute of Standards and Technology) was analyzed every 12–15 samples to enable quantification and correction of possible instrumental drift. Correction for gas blank and drift effects and conversion of raw isotopic counts to elemental concentrations (μg/g) were performed using a Microsoft Excel macro developed at GLIER (Chapman et al. 2013). Concentrations of strontium, barium, and magnesium were converted to molar element:calcium ratios (Sr:Ca, Ba:Ca, or Mg:Ca; μmol/mol) using calcium as an internal standard and the stoichiometric concentration of calcium in aragonite (400,436 µg Ca g^{-1} $CaCO_3$). Molar Mg:Ca ratio was used in conjunction with Ba:Ca and Sr:Ca data as an indicator of the potential presence of vaterite (a crystalline form of $CaCO_3$ that differs in affinity for Mg, Ba, and Sr compared to aragonite; Melancon et al. 2005; Veinott et al. 2009) in otolith samples. Otolith Mg:Ca > 400 µmol/mol in combination with Sr:Ca < 100 µmol/mol and Ba:Ca < 4 µmol/mol was considered indicative of the potential presence of vaterite. Data from any fish that exhibited these combinations of otolith core Mg:Ca, Sr:Ca, and Ba:Ca were excluded from further analyses to avoid potential misinterpretation of early-life environment, as data from vateritic and aragonitic otoliths are not directly comparable (Melancon et al. 2005).

Data analyses

To assess differences in mean water Sr:Ca, Ba:Ca, and δ^{18}O among rivers or river reaches, one-way analyses of variance followed by Tukey's honestly significant differences tests for multiple comparisons were conducted. An upstream–downstream gradient in water δ^{18}O was apparent for samples collected from the UMR, but not for Sr:Ca or Ba:Ca. Therefore, data from water sampling locations in the UMR upstream and downstream of LD19 were separated into 'upriver' and 'downriver' groups for analysis of spatial differences in mean water δ^{18}O but were combined into a single 'UMR' category for assessment of differences in mean water Sr:Ca and Ba:Ca among potential locations used during early life for bigheaded carps.

Identification of environments used during early life by adult Bighead Carp and Silver Carp collected from Pools 19–21 of the UMR using otolith core Sr:Ca, Ba:Ca and δ^{18}O required characterization of the ranges of otolith Sr:Ca, Ba:Ca and δ^{18}O signatures representative of each environment potentially used by age-0 bigheaded carps. Bigheaded carp of known origin were not available for characterization of location-specific otolith chemical signatures due to the open, connected nature of the river systems in our study area and propensity for movement by bigheaded carps (including downstream drift by age-0 fish and volitional movement by older individuals). Therefore, ranges of otolith chemical signatures for each potential early-life environment for bigheaded carps in our study area were estimated using water chemistry data and relationships between water and otolith chemistry parameters for bigheaded carps. Water chemistry data across all years and months were combined and minimum and maximum values for each water-chemistry parameter (Sr:Ca, Ba:Ca and δ^{18}O) were determined for each river or river segment (water δ^{18}O data from the UMR upstream and downstream of LD19 were considered separately in this analysis). The range of values for each water-chemistry parameter from each river or river segment were entered into linear regression equations relating water and otolith chemistry for bigheaded carps (Norman and Whitledge 2015) and 95% confidence limits for predicted otolith Sr:Ca, Ba:Ca, and δ^{18}O values corresponding to each water value were calculated. The 95% confidence limits around predicted Sr:Ca, Ba:Ca, and δ^{18}O values served as estimates of thresholds that defined the upper and lower limits of expected bigheaded carp otolith Sr:Ca, Ba:Ca and δ^{18}O for each river (or river segment in the case of predicted otolith δ^{18}O for the UMR upstream versus downstream of LD19). Predicted ranges of otolith Sr:Ca, Ba:Ca and δ^{18}O signatures for each river or river segment were then used to define early-life environment categories for bigheaded carps in the study area (a location or group of locations with distinct combinations of otolith Sr:Ca, Ba:Ca, and δ^{18}O); most categories included more than one river or river segment due to partial overlap in ranges of predicted otolith chemistry signatures among several pairs of rivers or river segments.

Each individual Bighead or Silver Carp collected from the UMR was assigned an early-life environment category using its otolith core Sr:Ca, Ba:Ca and δ^{18}O values (the portion of the otolith that reflects early life history). Early-life environment category assignment and collection location were used to infer upstream or downstream passage through the lock chamber at LD19 by individual fish when possible (e.g., a fish captured in Pool 19 and was assigned to an early-life environment category that included only locations downstream of LD19 was identified as an individual that had passed upriver through the lock). Chi square tests were used to assess whether relative frequencies of individuals with early-life otolith chemical signatures reflective of locations upstream versus downstream of LD19 differed between fish collected in Pool 19 and fish collected in Pools 20 and 21; separate analyses were conducted for each species.

P values ≤ 0.05 were considered significant for all statistical tests.

Results

Differences in water Sr:Ca, Ba:Ca, and $\delta^{18}O$ were present among environments potentially occupied during age-0 by bigheaded carps collected from Pools 19–21 of the UMR. Mean water Sr:Ca differed among rivers ($F_{9,183} = 54.72$, $P < 0.0001$); water Sr:Ca values > 2 mmol/mol were present only in the Missouri, Middle Mississippi, and Des Moines rivers and occasionally in the Illinois River, whereas maximum observed water Sr:Ca in the UMR was 1.67 mmol/mol (Fig. 2a). Mean water Sr:Ca for the UMR was not significantly different from some of its tributaries (Salt, Skunk, Iowa and Cedar rivers), although water Sr:Ca was lower in the Rock River compared to the UMR (Fig. 2a). Mean water Ba:Ca also differed among rivers ($F_{8,81} = 63.69$, $P < 0.0001$); water Ba:Ca values > 0.4 mmol/mol occurred exclusively in the Missouri and Middle Mississippi rivers and tributaries to the UMR that enter from the west (Skunk, Iowa, Cedar, and Des Moines rivers; Fig. 2b). Mean water $\delta^{18}O$ also differed among environments potentially used during age-0 by bigheaded carps ($F_{9,160} = 29.24$, $P < 0.0001$), although overlap in ranges of water $\delta^{18}O$ values among rivers was generally greater in comparison to Sr:Ca (Fig. 3). Sampling sites in the UMR upstream of LD19 had significantly lower (more negative) mean water $\delta^{18}O$ compared to the UMR downstream of LD19, although the ranges of water $\delta^{18}O$ values for 'upriver' and 'downriver' sites overlapped (Fig. 3). Water $\delta^{18}O$ values > -5.3‰ were solely associated with tributaries whose confluences with the UMR are downstream of LD19 (Illinois, Salt, and Des Moines rivers; Fig. 3). Differences in distributions of water Sr:Ca, Ba:Ca, and $\delta^{18}O$ among several rivers or river segments allowed some locations or groups of locations to be distinguished from one another using Sr:Ca, Ba:Ca, and $\delta^{18}O$ in combination and thus enabled development of an early-life environment classification model for bigheaded carps based on predicted ranges of otolith Sr:Ca, Ba:Ca, and $\delta^{18}O$ signatures (Table 1).

Most adult Bighead Carp collected from Pools 19–21 had otolith core chemical signatures indicative

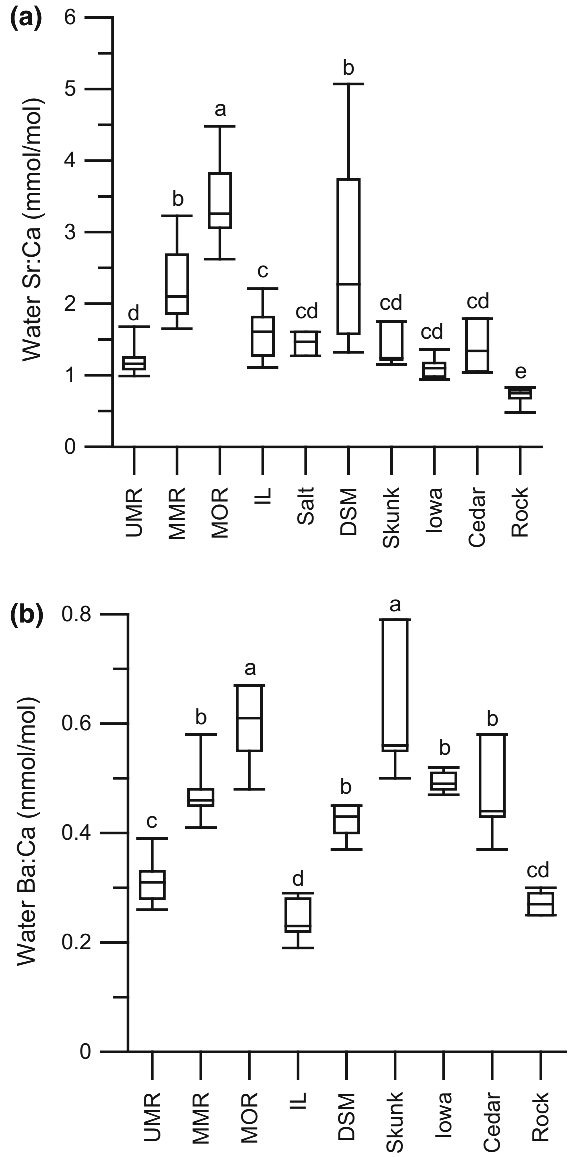

Fig. 2 Boxplots displaying the ranges, medians, and interquartile ranges for **a** water Sr:Ca and **b** water Ba:Ca from rivers potentially used during early life by Bighead Carp and Silver Carp collected in Pools 19–21 of the Upper Mississippi River. *UMR* Upper Mississippi River, *MMR* Middle Mississippi River, *MOR* Missouri River, *IL* Illinois River, *DSM* Des Moines River. Mean water Sr:Ca or Ba:Ca differ among locations that do not bear the same letter above boxplots (ANOVA followed by Tukey's HSD test, $P < 0.05$)

of use of environments downstream of LD19 during age-0 (Table 2). The relative frequency of Bighead Carp with otolith core chemical signatures reflective of upstream versus downstream of LD19 did not differ between fish collected in Pool 19 and in Pools 20 and

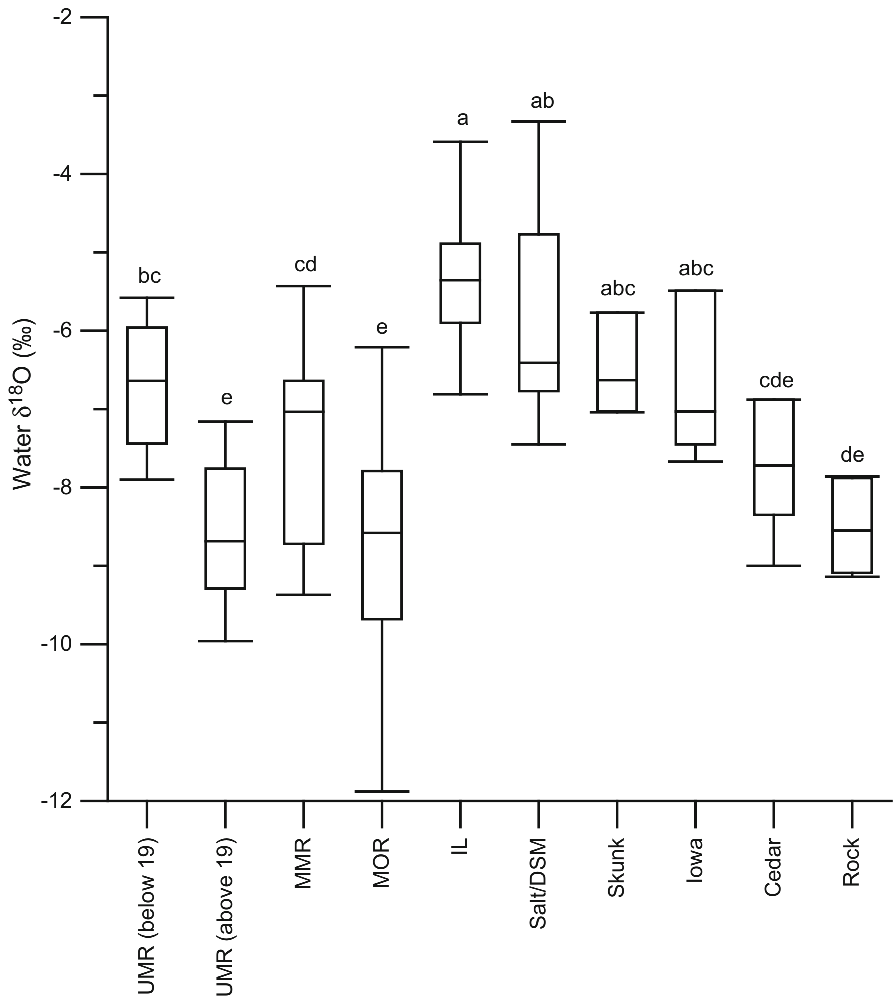

Fig. 3 Boxplot displaying the ranges, medians, and inter-quartile ranges for water $\delta^{18}O$ from rivers potentially used during early life by Bighead Carp and Silver Carp collected in Pools 19–21 of the Upper Mississippi River. For the Upper Mississippi River (UMR), data for locations upstream and downstream of Lock and Dam 19 are plotted separately. *MMR* Middle Mississippi River, *MOR* Missouri River, *IL* Illinois River, *DSM* Des Moines River. Locations that do not bear the same letter above boxplots have significantly different mean water $\delta^{18}O$ (ANOVA followed by Tukey's HSD test, $P < 0.05$)

21 ($\chi^2 = 4.35$, $P = 0.11$). Among the 21 Bighead Carp collected from Pool 19, twelve had passed upriver through the lock chamber at LD19 based on their predicted early-life environment being downriver from LD19. Two Bighead Carp collected from Pool 19 had otolith core chemical signatures characteristic of the Skunk/Iowa/Cedar rivers category. There were 10 Bighead Carp (6 captured upstream of LD19 and 4 captured downstream of LD19) for which the location of their early-life environment in relation to LD19 could not be determined from their otolith core chemical signature. One Bighead Carp had otolith core Mg:Ca (476 µmol/mol), Sr:Ca (91 µmol/mol), and Ba:Ca (3 µmol/mol) consistent with the vaterite crystalline form of $CaCO_3$. Although it is possible that otolith core chemistry for this fish may have reflected use of a location with high Mg:Ca, low Sr:Ca, low Ba:Ca, and $\delta^{18}O$ about − 3‰, none of the rivers in the study area (Table 1) nor other tributaries of the UMR or the Middle Mississippi River would be expected to yield the combination of otolith Mg:Ca, Sr:Ca, Ba:Ca, and $\delta^{18}O$ values observed for this fish (Zeigler and Whitledge 2010, 2011; Norman and Whitledge 2015; Whitledge, unpublished data). Due to a suspected vateritic otolith core, an early-life environment was not assigned to this fish and data from this individual were excluded from statistical analysis.

In contrast to Bighead Carp, the relative frequency of Silver Carp with otolith core chemical signatures reflective of locations upstream versus downstream of LD19 differed between fish collected in Pool 19 and Pools 20 and 21 ($\chi^2 = 16.44$, $P < 0.05$). Seventy-six percent of Silver Carp sampled from Pools 20 and 21 (66 of 87 fish) had otolith core signatures indicative of

Table 1 Categorization of potential early-life environments for bigheaded carps collected from Pools 19–21 of the Upper Mississippi River (UMR) based on predicted ranges of otolith Sr:Ca, Ba:Ca and $\delta^{18}O$ in combination

Early-life environment	Predicted combination of otolith chemistry values that distinguish location
Downstream of LD19	
UMR downstream of LD19 or tributary downstream of LD19	Sr:Ca 55–894 µmol/mol and Ba:Ca < 30 µmol/mol and $\delta^{18}O$ − 6.45‰ to − 7.4‰
Tributary downstream of LD19	Sr:Ca 235–1554 µmol/mol and Ba:Ca < 30 µmol/mol and $\delta^{18}O$ > − 6.45‰
Middle Mississippi or Des Moines River	Sr:Ca 895–2034 µmol/mol and Ba:Ca < 40 µmol/mol and $\delta^{18}O$ − 6.45‰ to − 7.6‰
Des Moines River	Sr:Ca > 1075 and $\delta^{18}O$ > − 6.45‰
Middle Mississippi River	Sr:Ca 895–2034 µmol/mol and $\delta^{18}O$ < − 7.6‰
Middle Mississippi or Missouri River	Sr:Ca 2035–2790 µmol/mol and $\delta^{18}O$ − 7.6‰ to − 9.3‰
Missouri River	Sr:Ca > 2035 µmol/mol and $\delta^{18}O$ < − 9.3‰ *or* Sr:Ca > 2790 µmol/mol and $\delta^{18}O$ < − 7.6‰
Upstream of LD19	
Skunk, Iowa, or Cedar River	Sr:Ca 55–894 µmol/mol and Ba:Ca > 30 µmol/mol and $\delta^{18}O$ − 6.45‰ to − 8.0‰ *or* Sr:Ca 895–1074 µmol/mol and Ba:Ca > 40 µmol/mol and $\delta^{18}O$ − 6.45‰ to − 7.6‰
Rock River	Sr:Ca < 55 µmol/mol and $\delta^{18}O$ < − 8.0‰
UMR upstream of LD19	Sr:Ca 55–894 µmol/mol and Ba:Ca < 30 µmol/mol and $\delta^{18}O$ < − 8.0‰
Indeterminate relative to LD19	
UMR (either upstream or downstream of LD19) or tributary downstream of LD19	Sr:Ca 235–894 µmol/mol and Ba:Ca < 30 µmol/mol and $\delta^{18}O$ − 7.4‰ to − 7.6‰
UMR (either upstream or downstream of LD19)	Sr:Ca 55–234 µmol/mol and Ba:Ca < 30 µmol/mol and $\delta^{18}O$ − 7.4‰ to − 8.0‰ *or* Sr:Ca 235–894 µmol/mol and Ba:Ca < 30 µmol/mol and $\delta^{18}O$ − 7.6‰ to − 8.0‰

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locations downstream from LD19, whereas 28 of 63 fish captured in Pool 19 (44%) had otolith core chemical signatures reflective of environments used during early life that were downstream from LD19 (Table 3). Downstream passage through LD19 was inferred for 10 Silver Carp collected from Pools 20 and 21 based on their predicted early-life environment being upstream of LD19. Six Silver Carp collected from Pool 19 had an otolith core chemical signature reflective of the UMR upstream of LD19. Five Silver Carp collected from Pool 19 and one fish captured in Pool 20 had otolith core chemical signatures characteristic of the Skunk/Iowa/Cedar rivers category. Early-life environment of 35 Silver Carp in relation to LD19 could not be determined from their otolith core chemical signature.

Discussion

Otolith core chemistry for bigheaded carps sampled from Pools 19–21 of the UMR during 2013–2014 indicated that multiple sources of recruits have contributed to the upriver expansion of bigheaded carps in the UMR. Control of bigheaded carp abundance in the UMR management zone (Pools 16–19) would likely be most efficient and effective if control strategies account for the combined set of locations that have contributed recruits to expanding bigheaded carp populations. Inferred early-life environments of bigheaded carps sampled from Pool 19 included locations upstream and downstream of LD19. Thus, sustainable control of bigheaded carp abundance in Pool 19 will likely require efforts to control reproduction and recruitment upstream of LD19 and immigration from downriver.

Table 2 Distribution of early-life environments for adult Bighead Carp collected from Pool 19 and Pools 20–21 of the Upper Mississippi River (UMR) during 2013–2014 inferred from otolith core Sr:Ca, Ba:Ca and $\delta^{18}O$

Inferred early-life environment	Collection location	
	Pool 19	Pools 20–21
Downstream of LD19		
UMR downstream of LD19 or tributary downstream of LD19	6 (30)	4 (16)
Tributary downstream of LD19	4 (20)	15 (60)
Middle Mississippi or Des Moines River	2 (10)	0
Des Moines River	0	0
Middle Mississippi River	0	0
Middle Mississippi or Missouri River	0	2 (8)
Missouri River	0	0
Upstream of LD19		
Skunk, Iowa, or Cedar River	2 (10)	0
Rock River	0	0
UMR upstream of LD19	0	0
Indeterminate relative to LD19		
UMR (either upstream or downstream of LD19) or tributary downstream of LD19	6 (30)	4 (16)
UMR (either upstream or downstream of LD19)	0	0

Values represent number of individuals collected in each location that were assigned to each environmental category (percentage of total number of individuals from each location in parentheses)

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Otolith chemistry data also indicated that tributaries to the UMR, including the Skunk, Iowa, or Cedar rivers and tributaries downstream of LD19, have contributed to bigheaded carp recruitment in Pools 19–21 of the UMR. Bigheaded carp spawning and presence of eggs and larvae have been documented in the Illinois River (Degrandchamp et al. 2007); a previous otolith chemistry study indicated that the Illinois River itself is the principal recruitment source for bigheaded carps present there (Norman and Whitledge 2015). Bigheaded carps have a propensity to move long distances and often move between the Illinois and Mississippi rivers (Degrandchamp et al. 2008; Lubejko et al. 2017). Thus, some contribution of the Illinois River as a source of bigheaded carp recruits to the UMR would not be surprising. Bigheaded carp eggs and larvae have also been observed in the Iowa, Skunk, and Des Moines rivers, albeit less commonly than in the UMR (Camacho 2016; Larson et al. 2017). Temporary movement by adult bigheaded carps from the UMR into the Skunk and Iowa rivers during time periods when environmental conditions were conducive to spawning have been documented using telemetry (K. Mosel, U.S. Fish and Wildlife Service, unpublished data). Otolith chemistry data provide evidence that UMR tributaries have contributed to bigheaded carp recruitment in the UMR, although assessment of the relative importance of individual tributaries as environments used by early-life stages of bigheaded carps is precluded by substantial overlap in water chemistry signatures among these tributaries. Continued monitoring of the UMR and tributaries to document times and locations of bigheaded carp reproduction and further application of otolith chemistry to infer spatial and temporal patterns of environments used during early life for emerging bigheaded carp populations will be useful for understanding factors influencing reproductive success and recruitment of invasive bigheaded carps.

The relatively high frequency of bigheaded carps with otolith core chemical signatures reflective of locations downstream of LD19 among individuals sampled from Pools 19–21 during 2013–2014 may be partly due to the size (and probable age) distribution of

Table 3 Distribution of early-life environments for adult Silver carp collected from Pool 19 and Pools 20–21 of the Upper Mississippi River (UMR) during 2013–2014 inferred from otolith core Sr:Ca, Ba:Ca and $\delta^{18}O$

Inferred early-life environment	Collection location	
	Pool 19	Pools 20–21
Downstream of LD19		
UMR downstream of LD19 or tributary downstream of LD19	13 (21)	17 (20)
Tributary downstream of LD19	1 (1)	21 (24)
Middle Mississippi or Des Moines River	8 (13)	14 (16)
Des Moines River	0	0
Middle Mississippi River	5 (8)	9 (10)
Middle Mississippi or Missouri River	1 (1)	4 (5)
Missouri River	0	1 (1)
Upstream of LD19		
Skunk, Iowa, or Cedar River	5 (8)	1 (1)
Rock River	0	0
UMR upstream of LD19	6 (10)	9 (10)
Indeterminate relative to LD19		
UMR (either upstream or downstream of LD19) or tributary downstream of LD19	16 (25)	8 (9)
UMR (either upstream or downstream of LD19)	8 (13)	3 (4)

Values represent number of individuals collected in each location that were assigned to each environmental category (percentage of total number of individuals from each location in parentheses)

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fish included in this study. Based on the size distribution of fish collected, most fish sampled for this study were likely $\geq$ age-3 (Camacho et al. 2016), and thus represented individuals from 2011 and earlier year classes. Thus, our data suggest that successful spawning and recruitment of bigheaded carps upstream of LD19 likely began in 2011 or earlier. In 2016, targeted surveys documented substantial numbers of age-0 bigheaded carps in Pool 19, providing the first direct evidence of a strong year class of bigheaded carps upstream of LD19 (J. Lamer unpublished data). Therefore, relative contributions of recruitment sources upstream and downstream of LD19 inferred for bigheaded carps sampled in Pool 19 during 2013–2014 for this study may not be indicative of the current relative contribution of locations upstream of LD19 to bigheaded carp recruitment in the UMR bigheaded carp management zone. Further application of otolith chemistry, particularly for fish collected upstream of LD19, would be valuable to assess whether recruitment sources supporting emerging bigheaded carp populations upstream of LD19 have changed over time, particularly following the apparently strong year class in 2016.

Elemental concentrations and stable isotope ratios of water samples collected for this study were consistent with previously published values from the UMR, tributaries, and the Missouri and Middle Mississippi rivers (Coplen and Kendall 2000; Kelly et al. 2001; Winston and Criss 2003; Zeigler and Whitledge 2011). Consistency of water Sr:Ca, Ba:Ca, and $\delta^{18}O$ data here and in previous studies suggests that differences in water chemistry among rivers or river reaches are relatively stable over time. Differences in bedrock geology among watersheds likely account for observed differences in Sr:Ca and Ba:Ca among rivers (Zeigler and Whitledge 2011; Pracheil et al. 2014), whereas a latitudinal gradient in precipitation $\delta^{18}O$ (Kendall and Coplen 2001) is likely responsible for spatial differences in water $\delta^{18}O$ in the UMR.

Despite partial overlap in ranges of water Sr:Ca, Ba:Ca, and $\delta^{18}O$ among pairwise combinations of rivers or river segments, sufficient spatial differences in multivariate water chemistry signatures were present to enable development of a classification model for inferring environments occupied during early life by bigheaded carps sampled from Pools 19–21 of the UMR. The occurrence of water chemistry signatures (Sr:Ca, Ba:Ca, and δ^{18}O in combination) characteristic of particular rivers, river segments, or groups of rivers in the study area despite some intra- and inter-annual variability in water chemistry within sites permitted development and application of the early-life environment classification model to individual fish regardless of year class. Thus, the early-life environment classification model will likely be applicable to future calcified structure chemistry studies on bigheaded carps in the lower portion (Pools 16 and downriver) of the UMR. However, continued monitoring of water chemistry will be needed to verify that differences in water Sr:Ca, Ba:Ca, and δ^{18}O among rivers and differences in water δ^{18}O within the UMR persist. If evidence of reproduction upstream of LD15 becomes evident, water sampling in UMR tributaries upstream of LD15 will be required to characterize their water Sr:Ca, Ba:Ca, and δ^{18}O signatures; incorporation of these upstream tributaries as potential locations used during early life will also be required. An increase in the number of potential natal rivers would likely increase uncertainty in early-life environment assignment for individual fish due to potential overlap in water chemistry between sites sampled in this study and UMR tributaries upstream of LD15. We also anticipate that differences in water chemistry among the UMR and tributaries documented in this study will be applicable to studies using calcified structure chemistry to infer environmental history of other fish species, although such studies will need to account for differences in relationships between water and calcified structure chemistry between bigheaded carps and other riverine fish species (Zeigler and Whitledge 2010; Norman and Whitledge 2015).

Application of otolith chemistry for inferring early-life environment and LD19 passage for bigheaded carps could prove useful for monitoring effects of current and potential control measures intended to reduce abundance of these species upstream of LD19. Contracted commercial fishing is being used to remove Bighead Carp and Silver Carp from Pool 19; placement of deterrents, such as carbon dioxide (Donaldson et al. 2016), broadband sound (Vetter et al. 2017), or bubble curtains (Zielinski and Sorensen 2016), in the lock chamber at LD19 are being considered to limit further immigration of bigheaded carps into Pool 19 from downriver. A combination of these approaches appears to be prudent based on otolith chemistry data from bigheaded carps indicating that Pool 19 contains individuals that used locations upstream of LD19 during early life and immigrants from downriver. Otolith chemistry could be useful for assessing the extent to which changes in bigheaded carp abundance in the UMR bigheaded carp management zone upstream of LD19 are associated with either changes in relative abundance of immigrants from downriver (e.g., due to installation of deterrents in the lock chamber at LD19 in combination with removal of prior immigrants via harvest in Pool 19) or recruitment of fish that used locations upstream of LD19 during their early life history.

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