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RECRUITMENT SOURCES OF CHANNEL AND BLUE CATFISHES INHABITING THE MIDDLE MISSISSIPPI RIVER

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ABSTRACT

Insight into environments that contribute recruits to adult fish stocks in riverine systems is vital for effective population management and conservation. Catfish are an important recreational species in the Mississippi River and are commercially harvested. However, contributions of main channel and tributary habitats to catfish recruitment in large rivers are unknown. Stable isotope and trace elemental signatures in otoliths are useful for determining environmental history of fishes in a variety of aquatic systems, including the Mississippi River. The objectives of this study were to identify the principal natal environments of channel catfish Ictalurus punctatus and blue catfish *I. furcatus* in the middle Mississippi River (MMR) using otolith stable oxygen isotopic composition (δ^{18} O) and strontium:calcium ratios (Sr:Ca). Catfishes were sampled during July-October 2013-2014 and lapilli otoliths were analyzed for δ^{18} O and Sr:Ca. Water samples from the MMR and tributaries were collected seasonally from 2006-2014 to characterize sitespecific signatures. Persistent differences in water $\delta^{18}O$ and Sr:Ca among the MMR and tributaries (including the upper Mississippi, Illinois, and Missouri rivers as well as smaller tributaries) were evident, enabling identification of natal environment for individual fish. Blue and channel catfish stocks in the MMR primarily recruited from the large rivers (Missouri and Mississippi) in our study area, with minimal contributions from smaller tributaries. Recruitment and year class strength investigations and efforts to enhance spawning and nursery habitats should be focused in the large rivers with less emphasis in smaller tributaries.

INTRODUCTION

Identifying critical habitats utilized by fishes for spawning, foraging, and refuge is vital for effective population management and conservation. Insight into environments and habitats that contribute recruits to adult stocks, as well as juvenile dispersal from natal environments, is important in understanding metapopulation dynamics (Hanski and Gilpin, 1997). However, information regarding spawning locations and early life stage dispersal are often limited and particularly challenging to obtain for species inhabiting large river systems (Phelps *et al.*, 2012). Many riverine species move significant distances for spawning, growth, and refuge (Fausch *et al.*, 2002), and understanding these movements and dispersal patterns is essential for developing the most appropriate spatial scales for management (Smith and Whitledge, 2011).

Large rivers and their tributaries offer a variety of habitats whose contributions to fish populations are not well understood. Alteration of geomorphic and hydrological complexity of large rivers through channelization, dredging, fragmentation, bank stabilization, and flow manipulation has contributed greatly to global declines of riverine species (Galat and Zweimüller, 2001). Tributaries may be important contributors to fish assemblages in large rivers, particularly at their confluences (Brown and Coon, 1994; Robinson *et al.*, 1998; Benda *et al.*, 2004). Tributaries that are less altered than the mainstem river may fulfill habitat and life history requirements of large-river fishes despite anthropogenic modification of mainstem habitat and flow regime (Neely *et al.*, 2009; Pracheil *et al.*, 2009). A recent study of distribution patterns of large-river specialist fishes in the Mississippi River basin found that tributaries above a threshold discharge (166 m³/s) contained \geq 80% of the local pool of these species; thus, relatively large tributaries represent potential focal areas for conservation of large-river specialist fishes (Pracheil *et al.*, 2013). However, the extent to which tributaries represent sources of recruits to large river fish populations, particularly species that are not large river specialists, is not well understood.

Catfishes are important recreational species in the Mississippi River and are commercially harvested (Pitlo, 1997). Channel catfish *Ictalurus punctatus* and blue catfish *I. furcatus* are native to the Mississippi River and occur in a wide variety habitats, but are characteristic of large, relatively turbid streams and rivers (Pflieger, 1997; Graham, 1999). Blue catfish are generally regarded as large-river specialists (Graham, 1999; Pracheil *et al.*, 2013), whereas channel catfish are more widely distributed and occupy habitats ranging from small rivers and impoundments to large rivers (Smith, 1979; Pflieger, 1997). Channel and blue catfishes may travel great distances in rivers for spawning and foraging (Graham, 1999; Hubert, 1999), and numerous telemetry studies have documented migratory behaviors and seasonal habitat use patterns of adults (Pugh and Schramm, 1999; Garrett and Rabeni, 2011; Tripp *et al.*, 2011). However, knowledge of the principal natal environments and early life habitat use and movement patterns for large river catfishes are limited.

Microchemical and stable isotopic analyses of fish otoliths are powerful techniques for addressing questions regarding environmental history of fishes in numerous freshwater environments, including the Mississippi River and tributaries (Zeigler and Whitledge, 2011; Phelps *et al.*, 2012; Norman and Whitledge, 2015). Trace element and stable isotopic compositions of otoliths reflect those of environments occupied by a fish (Kennedy *et al.*, 2002; Wells *et al.*, 2003), are unaltered metabolically following deposition (Campana and Thorrold, 2001), and serve as natural markers of environmental history of individuals. Association of otolith biochronology with elemental and isotopic composition enables retrospective description

of fish environmental history (including natal environment identification) when an individual has resided in chemically distinct locations for a sufficient period of time to incorporate the signature of those sites (Kennedy *et al.*, 2002; Whitledge *et al.*, 2007). Otolith chemistry has not been applied to identify recruitment sources of catfishes in large rivers. However, Smith and Whitledge (2011) validated relationships between water and catfish otolith trace elemental and stable isotopic compositions; data from a relatively small sample of catfishes from the Middle Mississippi River (MMR) were suggestive of multiple recruitment sources.

The goal of this study was to determine the principal natal environments of blue catfish and channel catfish in the MMR. Specific objectives were to verify that previously reported differences in water trace elemental and stable oxygen isotopic compositions among the MMR and its tributaries (Zeigler and Whitledge, 2010; Smith and Whitledge, 2011; Zeigler and Whitledge, 2011; Myers *et al.*, 2012; Phelps *et al.*, 2012) persisted across years and develop a classification model to identify natal river of individual catfish based on relationships between water and otolith trace elemental and stable isotopic compositions (Smith and Whitledge, 2011). Relative abundances of resident and immigrant origin catfishes were estimated, along with catfish movements between chemically distinct environments.

METHODS

Study area

The MMR is the unimpounded section of the river that extends 309 km from the mouth of the Missouri River (MOR) to the confluence of the Ohio River and supports recreational and commercial catfisheries. Our study area encompassed the entire MMR and included all major tributaries along this reach. Water samples were collected from 12 Mississippi River main stem and tributary locations (Figure 1). These locations included two sites in the upper Mississippi River (pool 25 and 26), two sites in the MMR (Thebes, IL, and Chester, IL), four tributaries of the Mississippi River on the Missouri side (Apple Creek, Headwater Diversion Channel, Meramec River, and MOR), and four tributaries of the Mississippi River on the Illinois side (Big Muddy River, Clear Creek, Illinois River, and Kaskaskia River). Fish sampling sites were divided among three reaches of the MMR to assess spatial differences in principal recruitment sources of catfishes (Figure 1). The first reach extends from the mouth of the MOR to the Kaskaskia River confluence and is influenced by three relatively large tributaries (Illinois River, MOR, and upper Mississippi River) with mean annual discharges greater than 651 m³/s and one smaller tributary (Meramec River) with a mean annual discharge of 92 m³/s (USGS 2015a, 2015b). The second reach of the MMR extends from the Kaskaskia River confluence to Big Muddy River confluence; this reach is influenced by a single tributary (Kaskaskia River) with a mean annual discharge of 109 m³/s (USGS 2015a). The third reach ranges from the mouth of the Big Muddy River to the Ohio River confluence and is influenced by relatively small tributaries (Apple Creek, Clear Creek, and Headwater Diversion Channel) with mean annual discharges of less than 14 m³/s and the Big Muddy River with a mean annual discharge of 60 m³/s (USGS 2015a, 2015b).

Water collection and analyses

Duplicate 20-mL water samples for strontium and calcium concentrations (for calculation of Sr:Ca ratios) and stable oxygen isotopic composition were collected from each site (Figure 1) during June-October 2013 and 2014 to verify persistence of differences in stable isotopic and

elemental signatures among the Mississippi River and its tributaries that were present during 2006-2012 (Zeigler and Whitledge, 2010, 2011; Smith and Whitledge, 2011; Myers *et al.*, 2012; Phelps *et al.*, 2012; Norman and Whitledge, 2015). Water samples for stable oxygen isotope analysis were collected in scintillation vials and sealed with Parafilm® to restrict evaporative loss and fractionation (Kendall and Caldwell, 1998). Samples were analyzed for stable oxygen isotopic composition using a high-temperature conversion elemental analyzer (TC/EA) interfaced with a Thermo Finnigan Delta $V^{\text{®}}$ isotope ratio mass spectrometer at the Southern Illinois University Mass Spectrometry Facility. Stable oxygen isotope ratios were expressed in the standard delta (δ) notation, defined as the parts per thousand (ppt) deviation between the isotope ratio of a sample and standard material (Vienna Standard Mean Ocean Water for water $\delta^{18}O$):

$$\delta^{18}O$$
 (%0) = $[(R_{\text{sample}} / R_{\text{standard}}) - 1] \times 1000;$

where *R* represents ¹⁸O/¹⁶O. Analytical precision estimated from analysis of laboratory standards was 0.07‰. Water samples for analysis of strontium and calcium concentrations were filtered using acid-cleaned polypropylene syringes and Whatman Puradisc 0.45-μm polypropylene syringe filters (Shiller, 2003; Rude *et al.*, 2014) and refrigerated until over-night shipment and analysis at the Center for Trace Analysis, University of Southern Mississippi. Following acidification and dilution of water samples in the laboratory (Rude *et al.*, 2014), samples were analyzed for ⁴⁴Ca and ⁸⁸Sr in high resolution using a Thermo-Finnigan Element 2 (Thermo Fisher Scientific, Waltham, MA, USA) inductively coupled plasma mass spectrometer (ICPMS). Precision of analysis based on repeated measurements of standards was better than ± 2% (2 SD). Elemental concentration data for water samples were converted to molar Sr:Ca ratios (mmol/mol).

Otolith preparation and analyses

Blue catfish and channel catfish were collected from six sites in the MMR (Figure 1) during summer 2013 and 2014 using low-pulse DC electrofishing, trawls (Herzog *et al.*, 2005) and hoop nets. Individuals in our sample were less than 545 mm TL (< age 8) to allow direct comparison with water chemistry data; fish exceeding this length may represent individuals old enough to be from year classes (Pflieger, 1997; Oliver, unpublished data) outside the range of years for which we have water chemistry data for the MMR and tributaries (2006-2014). Catfishes were euthanized with MS-222, placed on ice during transport back to the laboratory, and stored frozen until otolith removal.

Lapilli otoliths were removed from each fish by sectioning through the supraoccipital bone 3-5 mm anterior to the base of the pectoral fins (Buckmeier *et al.*, 2002; Smith and Whitledge, 2011). Otoliths were extracted using nonmetallic forceps, rinsed with distilled water, and stored dry in polyethylene microcentrifuge tubes until further analysis. One otolith from each fish was analyzed for stable oxygen isotopic composition. Whole otoliths from young-of-year (YOY) individuals were pulverized with a mortar and pestle to provide a fine powdered sample for analysis. Otoliths from older juveniles and adults were embedded in Epo-fix epoxy (Electron Microscopy Sciences Inc., Hatfield, PA), sectioned in the transverse plane using a Buehler ISOMETTM (Buehler Inc., Lake Bluff, IL, USA) low-speed saw, sanded using silicon carbide sandpaper (800 and 1000 grit) to obtain a 1.3-1.5 mm section centered on the otolith nucleus, and polished with lapping film. Sectioned otoliths were mounted on acid-washed glass microscope slides using cyanoacrylate glue. Approximately 300 µg of powdered sample was drilled from the

nucleus (reflecting natal environment) of each sectioned otolith using a New Wave Research (Portland, OR) micromill and stored in Labco Exetainer (Labco, Ltd., Lampeter, UK) tubes. Stable oxygen isotope analysis of otolith subsamples was conducted using a ThermoFinnigan Delta V^{\otimes} isotope ratio mass spectrometer interfaced with a Gas Bench II^{\otimes} (Thermo Fisher Scientific, Waltham, MA, USA) carbonate analyzer. 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 otolith from each fish was used for analysis of Sr:Ca. Otoliths from YOY fish were mounted whole on acid-washed glass microscope slides using cyanoacrylate glue, sanded (1000 grit) in the sagittal plane to reveal the nucleus, ultrasonically cleaned for 5 minutes in ultrapure water, and dried for 24 h under a laminar flow hood. Similarly, otoliths from larger juveniles and adults were prepared as described above for stable oxygen isotope analysis, but were sanded (800 and 1000 grit) to achieve a 0.5-0.7 mm section revealing annuli, mounted to microscope slides using double-sided tape, cleaned and dried as described for YOY Sr:Ca otoliths, and stored in acid-washed polypropylene Petri dishes. Sectioned and whole otoliths were analyzed for strontium and calcium concentrations using a Perkin-Elmer DRC II (Perkin-Elmer Life and Analytical Sciences, Shelton, CT, USA) inductively coupled plasma mass spectrometer (ICPMS) coupled with a CETAC Technologies (Teledyne CETAC Technologies, Omaha, NE, USA) LSX-213 laser ablation system. The laser ablated a transect extending from one side of the otolith core to the edge of the opposite side of the otolith (beam diameter = 100 μ m, scan rate = 5 μ m/s, laser pulse rate = 10 Hz, laser energy level = 75%, wavelength = 266 nm). A standard developed by the U.S. Geological Survey (MACS-3; CaCO₃ matrix) was analyzed by laser ablation every 15-20 samples to adjust for possible instrument drift. Each sample analysis was preceded by a 30 s gas blank measurement. Isotopic counts were converted to elemental concentrations (µg/g) after correction for gas blank, matrix, and drift effects (Ludsin et al., 2006). Mean limit of detection for ⁸⁸Sr was 0.06 µg/g; concentrations of ⁸⁸Sr in all otoliths were well above the detection limit. Strontium concentration was normalized to calcium concentration based on the consideration of calcium as an internal standard and the stoichiometric calcium concentration in aragonite. Otolith microchemistry data are reported as Sr:Ca ratios (mmol/mol).

Movements between chemically distinct environments (Figure 4) were assessed by examining laser transect data (otolith core to edge) for shifts in otolith Sr:Ca indicative of interriver movement. For each fish, we quantified movement [0 (no movement) or 1 (movement)] within each year of life; species, year class, and age were documented. Age was estimated using incremental measurements corresponding to otolith annuli to assess year of life for individual catfish. Year class was obtained by subtracting the total number of increments by the year of capture.

Statistical analyses

One-way analyses of variance (ANOVAs) followed by Tukey's honestly significant differences (HSD) tests for multiple comparisons were conducted to assess differences in both mean water Sr:Ca and mean water δ^{18} O among sampling sites. Least-squares linear regressions were updated from Smith and Whitledge (2011) to characterize relationships between water and known otolith Sr:Ca and δ^{18} O; this included new water data from our sample period (Figure 3a, b). We combined water data among all years and seasons within a given site to calculate the 5^{th}

and 95th percentiles of water parameter data for each site using the MEANS procedure in SAS (SAS version 9.3, Cary, North Carolina).

Identification of natal environment for catfish collected in the MMR required classification of ranges of otolith Sr:Ca and $\delta^{18}O$ signatures representative of each potential natal environment. PROC GLM in SAS was used to calculate 95% confidence limits around predicted otolith Sr:Ca and $\delta^{18}O$ that corresponded to the 5th and 95th percentiles of water Sr:Ca and $\delta^{18}O$ for each natal environment category (MOR, Mississippi River, and tributaries; refer to Results) using the updated regression from Smith and Whitledge (2011) relating water and otolith Sr:Ca and $\delta^{18}O$ for catfishes. The 95% confidence limits around predicted otolith Sr:Ca and $\delta^{18}O$ values served as thresholds that defined the upper and lower limits of expected otolith Sr:Ca and $\delta^{18}O$ signatures for each natal environment (Figure 4). These ranges of expected otolith Sr:Ca and $\delta^{18}O$ values for each category were used to identify the natal environment of catfishes of unknown origin collected in the MMR. Natal environment was assigned to individual catfish by comparing otolith core Sr:Ca (first 25 μ m of laser ablation transects) and $\delta^{18}O$ with otolith Sr:Ca and $\delta^{18}O$ signature range limits defined for each category (Figure 4).

A loglinear model (Poisson and Negative Binomial distributions and log link) with a residual scale parameter was used to assess differences in frequencies of catfish from the three categories of potential natal environments (MOR, Mississippi River, or tributaries) between species, collection years (2013 and 2014), and river reach using the GLIMMIX procedure in SAS. Additionally, movement probabilities between chemically distinct environments were calculated for each year class within each species and assessed with logistic regression in a generalized linear model framework (Binomial distribution and logit link) using the GLIMMIX procedure in SAS. The Pearson Chi-Square divided by the degrees of freedom statistic (closest to 1) was used as the goodness-of-fit test for all models in conjunction with the Akaike information criterion values (smallest relative to other models). An $\alpha \leq 0.05$ was designated for all statistical tests.

RESULTS

Water chemistry parameters

Mean water Sr:Ca differed among river systems sampled during this study ($F_{9.119}$ = 68.82, p < 0.0001) with the highest water Sr:Ca occurring in the MOR (Figure 2a). The Big Muddy River and the MMR exhibited intermediate water Sr:Ca values while other tributary systems including the upper Mississippi River, Illinois River, Kaskaskia River, Meramec River, Apple Creek, Clear Creek, and the Headwater Diversion Channel showed the lowest Sr:Ca values. Similarly, mean water δ^{18} O values differed among the MMR and its tributaries ($F_{9.135}$ = 26.37, p < 0.0001) with the most negative water δ^{18} O value occurring in the MOR (Figure 2b). The upper Mississippi River and the MMR exhibited intermediate δ^{18} O values whereas the Illinois River, Kaskaskia River, Meramec River, Apple Creek, Clear Creek, and the Headwater Diversion Channel showed the least negative δ^{18} O values. Significant differences were observed between the MOR and all other river systems sampled in this study based on mean Sr:Ca and δ^{18} O values (Figure 2a,b). In general, the MMR was significantly different from its tributaries aside from the Big Muddy River based on Sr:Ca (Figure 2a) and the upper Mississippi River based on δ^{18} O (Figure 2b). Due to the inability to clearly distinguish certain tributary systems using water Sr:Ca and δ^{18} O, these tributaries (Illinois River, Clear Creek, Headwater Diversion Channel, Apple Creek, Big Muddy River, Kaskaskia River, and the Meramec River) were

combined to represent a single tributaries (TRB) category that was used in analysis of natal environment. Also, the MMR and upper Mississippi River could not be clearly distinguished with water δ^{18} O, resulting in these two systems being combined to represent the Mississippi River (MSR) as a natal environment category. Therefore, the MOR, MSR, and TRB represented the natal environment categories for unknown origin catfish collected in the MMR.

Relationships among water and otolith chemistry and natal environment classification

Otolith Sr:Ca from known environmental history catfishes was strongly correlated with water Sr:Ca values ($F_{1,27} = 198.50$, $R^2 = 0.88$, p < 0.0001; Figure 3a). Otolith δ^{18} O was also highly correlated with water δ^{18} O for catfishes of known environmental history ($F_{1,20} = 57.41$, $R^2 = 0.74$, p < 0.0001; Figure 3b).

Differences in water Sr:Ca and $\delta^{18}O$ among the MOR, MSR, and TRB systems and the highly significant linear relationship between water and known otolith Sr:Ca and $\delta^{18}O$ for catfishes enabled prediction of upper and lower 95% confidence limits for otolith Sr:Ca and $\delta^{18}O$ "signatures" characteristic of individuals that originated in each of these systems that could potentially supply recruits to catfish stocks in the MMR (Figure 4). Some overlap in predicted otolith signature limits for the three natal environment categories (MOR, MSR, and TRB) was present, resulting in some combinations of otolith Sr:Ca and $\delta^{18}O$ values that were not unique to a single natal environment category (Figure 4).

Natal environments of MMR blue and channel catfish

A total of 152 blue catfish and 175 channel catfish were collected from the MMR during summer 2013 and 2014 (Figure 1). No significant differences based on origin, collection year, and river reach were detected between species. However, slight differences among origins within species did occur: blue catfish: $Pearson \chi^2 / DF = 0.72$, $F_{5,10} = 27$, p < 0.0001; channel catfish: $Pearson \chi^2 / DF = 1.19$, $F_{5,10} = 5.57$, p = 0.0035. For blue catfish, the majority of our sample originated in the MOR (Figure 5a) with an estimated contribution of 53% to 68%. The MOR supplied significantly more recruits when compared to all other potential sources ($t_{10} = 5.02$ -7.24, $p \le 0.005$). The MSR was found to have an estimated contribution of 22% to 46% (Figure 5a) and supplied significantly more recruits than TRB ($t_{10} = 4.6$, p = 0.0092). Tributaries contributed the lowest percentage of individuals for blue catfish (1% to 11%; Figure 5a) and the frequency of fish in this category was significantly lower when compared to the MSR and MOR ($t_{10} = 4.6$; 6.11, p = 0.0092; 0.0012).

The MOR had an estimated contribution of 31% to 59%, whereas the MSR had an estimated contribution of 26% to 67% for channel catfish (Figure 5b); frequencies of channel catfish originating in these two natal environments were not significantly different. Tributaries contributed a smaller percentage of channel catfish (1 to 18%; Figure 5b) and the frequency of fish that originated in tributaries was significantly lower when compared to those that originated in the MSR and MOR ($t_{10} = 3.85$; 4.07, p = 0.0280; 0.0202).

Movements between chemically distinct environments

Movement probabilities of blue catfish were significantly higher than channel catfish $(F_{1,641} = 7.24, p = 0.0073)$. No significant interactions of species by year class, species by age, or species by year class by age were detected between species, resulting in similar movement probability patterns among species (Figure 6a, b). Within species, year class probabilities were

significantly different ($F_{6,641} = 6.57$, p < 0.0001) and year class by age probabilities were also significantly different ($F_{15,641} = 1.71$, p = 0.0453).

DISCUSSION

The influence of tributaries on recruitment of numerous fishes in large river networks has not been well documented. Large rivers support specialized fauna and often rely on a high degree of connectivity with large tributaries to meet the life history requirements of large-river specialist fishes (Neely et al., 2009; Pracheil et al., 2009; Pracheil et al., 2013). Relatively large tributaries (discharge ≥ 166 cubic meters per second) represent nearly all of the species richness present in mainstem rivers and provide opportunities for conserving large-river biota (Pracheil et al., 2013). In the present study, the majority of tributaries contributed minimal percentages of recruits to MMR blue and channel catfish stocks. Consistent with the findings presented in Pracheil et al. (2013), blue catfish (a large-river specialist) primarily recruited from the largest rivers in our study area and had minimal influence from smaller tributaries. Similarly, channel catfish (not a large-river specialist) recruited primarily from the largest rivers and less than 18% of individuals originated in smaller tributaries. This finding is somewhat surprising given the wider distribution of channel catfish in Missouri and Illinois compared to blue catfish (Smith, 1979; Pflieger, 1997) and suggests that the findings presented by Pracheil et al. (2013) regarding tributary size might apply to species other than large-river specialists. However, further research with other nonlarge-river specialist fishes in different river reaches is needed to determine the influence of tributary size on recruitment dynamics. Furthermore, future research into the habitat characteristics and utilization by channel catfish in smaller tributaries is needed to identify factors underlying the relatively small contribution of these small tributaries to channel catfish recruitment in the MMR, given that they are not a large-river specialist species.

Both blue and channel catfish stocks received a substantial contribution of recruits from the MOR. For blue catfish, the MOR contributed significantly more recruits than all other sources, whereas for channel catfish, the MOR was not significantly different from the Mississippi River. Several potential factors may be important in this finding. The MOR confluence defines the upper boundary of the MMR, and its influence as a recruitment source was consistent for each species among all three MMR reaches. This consistent influence of the MOR as a source of catfish recruits throughout the MMR is likely a result of its size and proximity to the MMR. Mean annual discharge for the MOR is 2,476 m³/s (USGS 2015b), more similar to that of the MMR than its other tributaries. This similarity may be more conducive for meeting the life history requirements of large river species such as catfish (Graham, 1999; Hubert, 1999). The MOR also contributes substantially to age-0 Scaphirhynchus sturgeons found in the MMR (Phelps et al., 2012), suggesting that the MOR may be an important recruitment source for a variety of fish species that occur in the MMR. The lower MOR and MMR are unimpounded reaches of each river (Phelps et al., 2012), promoting greater connectivity and exchange between these two systems, which may increase availability of habitats required by different life history stages of large river species such as catfish.

Closure of the commercial catfishery on the lower MOR may also explain the relatively high percentage of MMR catfishes that originated in the MOR. In an attempt to reallocate catfish resources to recreational users and alleviate overharvest, commercial harvest of catfishes in the lower MOR (i.e., the final 1,241 kilometers of the MOR) was closed in 1992 (Galat *et al.*, 1996). Numerous studies have shown that changes in both commercial and recreational fishing

regulations can positively impact catfish fisheries and increase mature fish abundance and recruitment (Pitlo, 1997; Colombo, 2007). Following the commercial harvest closure, the average length of catfishes in the MOR increased significantly and the standing crop of age 4-7 channel catfish increased to 58% in 1996-1997 (Mestl, 1999; Stanovick, 1999). Enhanced standing stocks and recruitment may partially account for the substantial export of recruits that from the MOR to the MMR. Our data suggest that the substantial influence of the MOR and minimal influence of other MMR tributaries on recruitment of MMR catfishes persists over time due to representation of multiple year classes (2008-2014) in our samples. These year classes represent hydrologically different years with discharge ranges varying among years both within and among river systems (USGS 2015a, 2015b). Thus, the observed patterns of catfish recruitment sources in the MMR are not solely reflective of very wet or very dry years. We were unable to explicitly test for differences in recruitment sources based on year class due to unequal sample sizes among year classes for each species. More extensive sampling of multiple year classes will be required to determine whether contributions of the potential natal environments (MOR, MSR, and TRB) examined in this study are consistent through time. In addition, other large river segments with relatively larger or more numerous tributaries may derive a higher portion of recruits from these systems for certain species, especially large-river specialist species (Pracheil et al., 2013), and continuing research in this area will aid in evaluating the ecological role of large river tributaries and how the MMR compares to other rivers and other sections of the Mississippi River.

Our data also provide evidence of exchange of catfishes between the MOR, MSR, and TRB environments despite certain limitations in our ability to describe specific movements of blue and channel catfish. Only a single otolith chemical marker (Sr:Ca otolith transect data) was used, resulting in a loss of resolution between chemically distinct environments. Our movement estimates are likely biased low as a result of individual catfish having to occupy an environment for a sufficient amount of time to record an environmental shift in the otolith. Unlike telemetry studies describing catfish movements (Garrett and Rabeni, 2011; Tripp et al., 2011), we were unable to describe the exact timing and distance of individual catfish movements. Blue catfish exhibited higher movement probabilities between the MOR and MSR/TRB environments compared to channel catfish, which is consistent with other studies describing the high mobility of blue catfish (Pugh and Schramm, 1999; Garrett and Rabeni, 2011; Tripp et al., 2011). Within each species, differences in movement probabilities existed between year classes and differed among ages within year classes. These differences in movement probabilities may be related to environmental variables such as water temperature and discharge that provide cues for catfish movements into overwintering and spawning sites (Pflieger, 1997; Graham, 1999). However, due to collinearity with other variables in our data, we were unable to test the effect of discharge on movement. Since both species display similar movement probability patterns across year classes and age (Figure 6a, b), it is likely that environmental cues have a strong influence. A long term data set encompassing multiple fish collection years and representing multiple year classes may aid in the ability of future research to detect the effects of discharge and temperature on catfish movements using otolith microchemistry.

The utility of otolith microchemistry and stable isotopic compositions as natural indicators of fish environmental history is dependent on the persistence of geographically based differences in water chemistry over time. Our results indicate that previously reported differences in water Sr:Ca and $\delta^{18}O$ among the middle Mississippi River and its tributaries

driven by differences in bedrock geology and hydrologic influences on water isotopic composition (Zeigler and Whitledge, 2010; Smith and Whitledge, 2011; Zeigler and Whitledge, 2011; Myers et al., 2012; Phelps et al., 2012) persisted over the 8-year time period from 2006-2014. Although some overlap in ranges of water Sr:Ca and δ^{18} O between the MMR and its tributaries occurred when data from 2006-2014 were combined, the distributions of water Sr:Ca and δ^{18} O for each of these systems were sufficiently different to yield broad ranges of water Sr:Ca and δ^{18} O values that were characteristic of a particular river (e.g., water Sr:Ca values > 2.6 mmol/mol were observed only in the MMR and MOR and only the MOR had water Sr:Ca values > 3.1 mmol/mol). Differences in water Sr:Ca and δ^{18} O among rivers that represented potential natal environments for blue catfish and channel catfish collected from the MMR enabled development and application of a single classification model to identify natal river for individual fish from otolith core Sr:Ca and δ^{18} O regardless of fish age. Moreover, we restricted the size of catfishes collected in this study to less than 545 mm total length (< age 8) (Pflieger, 1997) to include on those year classes for which water chemistry data were available throughout their lifetime. Because differences in water chemistry parameters have persisted for nearly a decade, our classification model will likely be applicable for identifying natal environments of older age classes of catfishes collected in the MMR in future years with continued monitoring of water Sr:Ca and δ^{18} O. In addition, the water chemistry data and the approach we used to develop our classification model will be applicable to other species in the MMR for which identification of principal recruitment sources is desired. However, characterization of relationships that are not yet available between otolith and water chemical signatures will be required for future study species due to differing relationships among taxa (Zeigler and Whitledge, 2010; Norman and Whitledge, 2015).

Localized management strategies are more likely to benefit fish that recruit from local sources and exhibit limited movement compared to more nomadic species (Pugh and Schramm, 1999). Blue catfish and channel catfish populations in the MMR recruit from multiple sources and receive a strong influence from the MOR and Mississippi River. As a result, management strategies aimed at protecting and maintaining these important recreational and commercial catfish populations should be implemented at a broad spatial scale. Stock assessments and population monitoring efforts for blue and channel catfish should include data from both the MMR and MOR, warranting a multijurisdictional management approach. Based on our finding of the minimal influence on recruitment from the smaller tributaries of the MMR, we should not expect these tributary systems to compensate for weak year classes produced in the MMR and MOR. Although these smaller tributaries seem to be less important in terms of recruitment, they may not necessarily be unimportant for use by other life history stages of catfishes. Several studies have indicated tributary use by older age classes in other systems that may correspond to increased feeding, growth, and survival (Garrett and Rabeni, 2011; Tripp et al., 2011). Small tributaries may provide prey subsidies to riverine fishes, and confluence areas could represent beneficial habitats even if small tributaries are not significant recruitment sources. Overall, efforts aimed at maintaining, protecting, or enhancing spawning and juvenile channel and blue catfish nursery habitats that support stocks of these species in the MMR, as well as recruitment and year class strength investigations, should be focused in the large rivers (MMR and MOR) themselves, with less emphasis on the smaller tributaries.

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FIGURE CAPTION LIST:

- **Figure 1.** Map of Mississippi River drainage in Illinois and Missouri showing locations where catfishes (open diamonds) and water samples (filled diamonds) were collected.
- **Figure 2.** Boxplots displaying the ranges, medians, and inter-quartile ranges for (a) water Sr:Ca and (b) water δ^{18} O from potential natal environments for blue and channel catfish in the middle Mississippi River; MMR = middle Mississippi River (Sr:Ca n = 20, δ^{18} O n = 26), UMR = upper Mississippi River (Sr:Ca n = 23, δ^{18} O n = 17), MOR = Missouri River (Sr:Ca n = 20, δ^{18} O n = 19), ILL = Illinois River (Sr:Ca n = 19, δ^{18} O n = 17), CCK = Clear Creek (Sr:Ca n = 10, δ^{18} O n = 11), HDC = Headwater Diversion Channel (Sr:Ca n = 9, δ^{18} O n = 8), ACK = Apple Creek (Sr:Ca n = 10, δ^{18} O n = 8), BMR = Big Muddy River (Sr:Ca n = 10, δ^{18} O n = 11), KAS = Kaskaskia River (Sr:Ca n = 10, δ^{18} O n = 8), MER = Meramec River (Sr:Ca n = 9, δ^{18} O n = 9), sampled June-October 2006-2014.
- **Figure 3.** Relationships between (a) otolith Sr:Ca and water Sr:Ca ($r^2 = 0.88$, p < 0.0001) and (b) otolith δ^{18} O and water δ^{18} O ($r^2 = 0.74$, p < 0.0001) for catfishes of known environmental origin.
- **Figure 4.** Predicted otolith values of the potential natal environments for MMR blue and channel catfish; MOR = Missouri River, MSR = Mississippi River, and TRB = Tributaries. Symbols represent overlap ranges among natal environments.
- **Figure 5.** Natal river for (a) blue catfish (n = 152) and (b) channel catfish (n = 175) collected from the MMR during 2013-2014 determined from otolith core Sr:Ca and δ^{18} O for individual fish. Values represent percentages of individuals collected that originated from each river (MOR = Missouri River; MOR/MSR = Missouri River or Mississippi River origin; MSR = Mississippi River; MSR/TRB = Mississippi River or Tributary origin; MOR/MSR/TRB = Missouri River, Mississippi River, or Tributary origin; TRB = Tributary origin).
- **Figure 6.** Movement probability patterns between chemically distinct environments (MOR and MSR/TRB) for (a) blue catfish and (b) channel catfish based otolith Sr:Ca transect data. Symbols represent year classes within each species and movement probability patterns correspond to ages of each respective year class.

Figure 1.

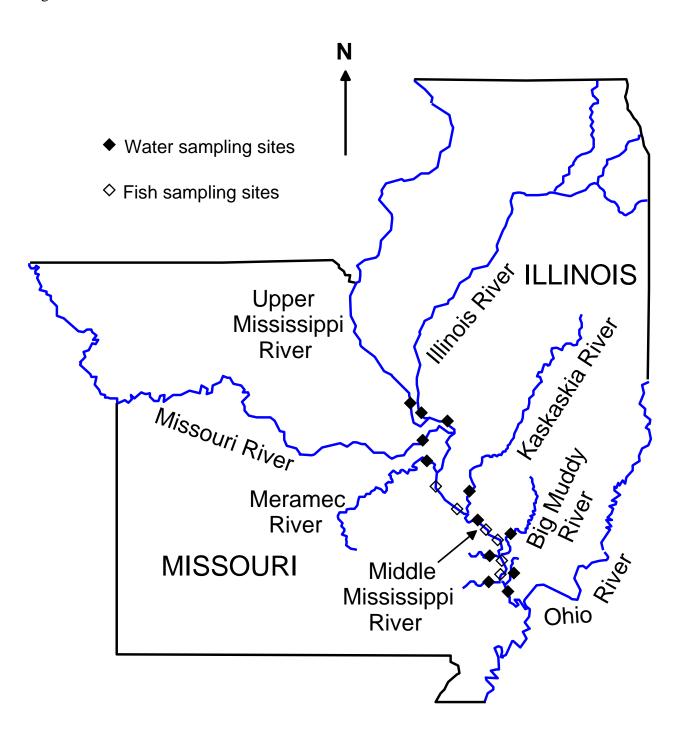


Figure 2.

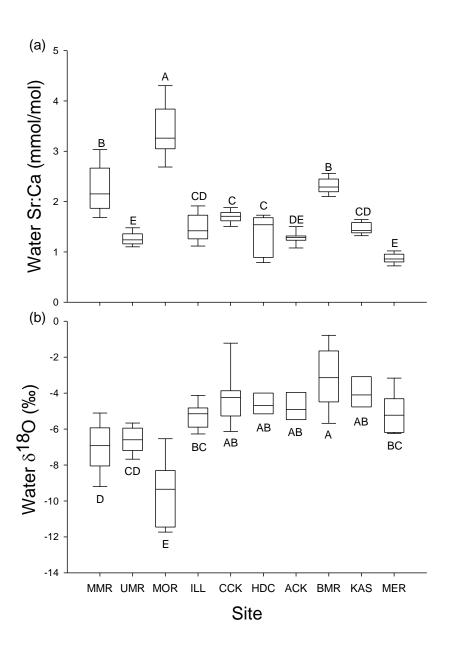


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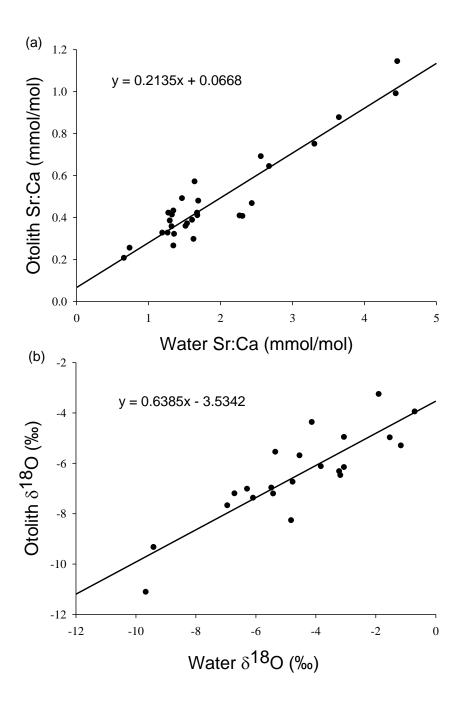


Figure 4.

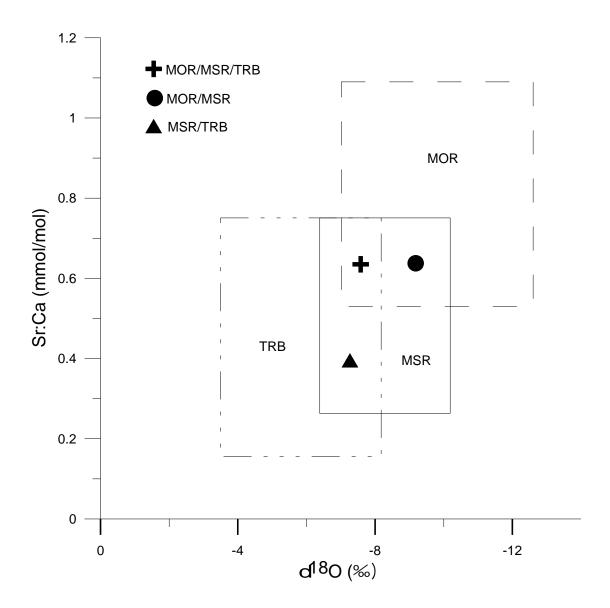
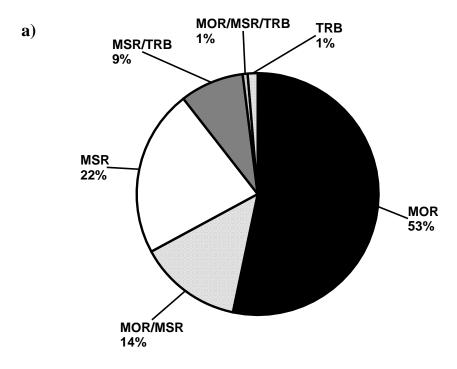


Figure 5.



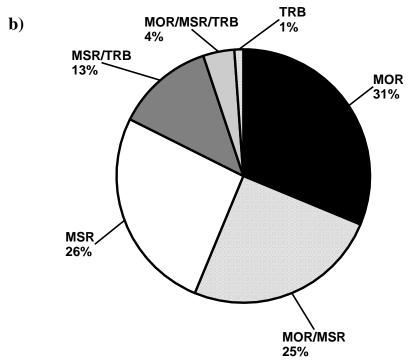


Figure 6.

