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ARTICLE

Otolith Microchemistry Reveals Natal Origins of Walleyes in Missouri River Reservoirs

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Abstract
Reproductive habitats are vital for sustaining fish populations, but their location and relative natal contributions are often unknown or poorly understood. We used otolith microchemistry to examine natal origins of Walleyes *Sander vitreus* in Missouri River reservoirs (i.e., Lake Oahe, Lake Sharpe, Lake Francis Case, and Lewis and Clark Lake) in North Dakota and South Dakota. Water Sr:Ca and Ba:Ca were spatially heterogeneous and temporally consistent in all impoundments. Otolith Sr:Ca and Ba:Ca from age-0 Walleyes permitted the reclassification of fish to known natal habitats (i.e., tributary, embayment, main stem) and individual sites with 87% and 75% accuracy, respectively. Natal contributions were highest in tributaries, particularly those in Lake Oahe, where 32% of all adults and 77% of Lake Oahe adults hatched. Embayments and main-stem environments had high natal contributions (67–78%) in Lakes Sharpe and Francis Case and Lewis and Clark Lake, where tributaries are less abundant. Our research demonstrates the utility of otolith microchemistry for measuring habitat- and site-specific natal contributions and provides further information that can be used in managing Walleyes in Missouri River reservoirs, particularly for broodstock collection, habitat protection and restoration, and harvest regulations.

Accurate identification of natal origins is necessary for the management of fish stocks that have multiple spawning locations (Papetti et al. 2013; Wirgin et al. 2015). However, knowledge of fish provenance is often confined to anecdotal patterns of natal site importance. This inhibits a manager's ability to prioritize locations for broodstock collection, habitat protection and restoration, harvest regulations, and other management activities. Identifying when and where reproduction occurs is particularly important when populations span multiple jurisdictions (Smith et al. 2005). Development of reliable methods for measuring natal contributions from different habitats and local sites would simplify stock discrimination and advance fisheries management.

Walleye *Sander vitreus* is an ecologically and socioeconomically important species throughout Canada and the United States (McMahon et al. 1984). Walleyes employ three general life history typologies: (1) river resident–river spawning, (2) lake resident–lake spawning, and (3) lake resident–river spawning (Bozek et al. 2011). Walleyes in reservoirs of the

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Missouri River use the lake resident–river spawning and lake resident–lake spawning strategies, as do populations in Lake Nipigon, Ontario (Dymond 1926), Oneida Lake, New York (Adams and Hankinson 1928), and the Laurentian Great Lakes (Wolfert 1963; Fielder et al. 2010). Adults select spawning sites with coarse substrates (Scott 1967; Grinstead 1971) to minimize egg siltation during hatching. They also prefer spawning sites with high fetch to increase water and oxygen flow over the eggs (Becker 1983; Martin et al. 2013). A number of habitats offer these conditions, including tributaries (Chalupnicki et al. 2010), flooded marshes (Priegel 1970), riverine portions of reservoirs (Quist et al. 2004), and riprap near reservoir dams (Grinstead 1971). However, estimating natal contributions from different habitats and local sites is difficult using traditional methods such as physical tagging (Bickford and Hannigan 2005) and genotyping (Eldridge et al. 2002). Thus, development of additional discrimination techniques in necessary and would advance Walleye management practices throughout North America.

Understanding the spatial distribution of Walleye spawning sites is important for habitat restoration and conservation planning throughout the species range, particularly in large, interconnected systems such as the Missouri River. However, provenance information is often limited to anecdotal evidence of tributary and embayment spawning accumulated during annual broodstock collection and population surveys (C. M. Longhenry, South Dakota Department of Game, Fish and Parks, personal communication). Thus, Missouri River managers are unable to measure site-specific natal contributions. A reliable method to quantify hatching magnitude and frequency would permit managers to classify natal locations by their importance. In turn, it would promote science-based management by enabling managers to prioritize specific sites where broodstock collection, habitat restoration (e.g., sediment dredging, riparian zone enhancement), harvest regulations, and other management strategies would be most effective.

Otolith microchemistry is an innovative tool for evaluating fish environmental history. It has been used throughout the world to investigate natal origins (Wolff et al. 2012; Rohtla et al. 2014), movement (Brenkman et al. 2007; Allen et al. 2009), and stock composition (Bickford and Hannigan 2005; Coghlan et al. 2007). Otoliths are paired calcified structures used for hearing and balance that form permanent depositions of certain trace elements, for example, strontium (Sr) and barium (Ba), in proportion to water column concentrations (i.e., signatures; Campana 1999; Campana et al. 2000). Combined with otolith biochronological properties (i.e., annuli), elemental accumulation permits retrospective assessment of environmental history throughout an individual's life provided water signatures are spatially heterogeneous. Large river systems such as the Missouri River tend to exhibit spatially variable, temporally stable water chemistry as signatures are influenced primarily by geology and weathering (Gibbs 1970; Bickford and Hannigan 2005). However, researchers often sample water in different time periods to verify temporal stability in water chemistry and ensure otolith microchemistry is a reliable tool for estimating site-specific natal contributions. This technique has rarely been used to identify Walleye natal origins in river systems (Bickford and Hannigan 2005; Pflugeisen and Calder 2013) and never in the Missouri River, where habitat- and site-specific natal contributions are poorly understood.

The goal of this study was to evaluate otolith microchemistry as an environmental history tool for advancing Walleye management in Missouri River reservoirs. Our objectives were to assess spatial and temporal patterns of trace element chemistry in waters of Missouri River reservoirs and tributaries, measure the relationship between water and Walleye otolith signatures, and assess habitat- and site-specific natal contributions. We hypothesized that water signatures would be spatially variable, temporally stable, and proportional to otolith signatures, thereby rendering otolith microchemistry a reliable environmental history tool. Anecdotal information has suggested that tributaries, particularly those in Lake Oahe, the largest of the Missouri River reservoirs, would be important natal sites.

METHODS

Study site.—The Missouri River is the longest river in North America, flowing 3,768 km from Brower's Spring, Montana, to its confluence with the Mississippi River just north of St. Louis, Missouri. The Missouri River watershed spans 1,371,017 km^2, the second-largest riverine drainage area in the United States, and encompasses 47 tributaries with drainage basins > 1,000 km^2 (Galat et al. 2005). The portion of the Missouri River in North Dakota and South Dakota is impounded into four reservoirs—Lake Oahe, Lake Sharpe, Lake Francis Case, and Lewis and Clark Lake—and spans a latitudinal gradient > 500 km. Lake Oahe measures 28.5 km^3 in volume, 1,263 km^2 in surface area, and 3,621 km in shoreline length, making it considerably larger than Lakes Sharpe (2.2 km^3, 231 km^2, 322 km) and Francis Case (6.7 km^3, 312 km^2, 869 km) and Lewis and Clark Lake (0.6 km^3, 97 km^2, 145 km) (Erickson et al. 2008). As a result of its larger size, Lake Oahe contains substantially more tributaries and embayments, commonly used by Walleyes as natal environments, than the other reservoirs. The study area is characterized by extensive spatial heterogeneity in surficial and bedrock geology. Cenozoic glacial sediments (e.g., Illinois and Wisconsin glacial sediments) predominate east of the Missouri River, whereas sediments are generally Mesozoic (e.g., sandstones, shales, clays) west of the river (SDDENR 2015).

Trace element sampling.—Water samples (n = 2–10/site) were collected from eight tributaries, six embayments, and three main-stem locations in Missouri River reservoirs in July–September 2012 to assess spatial patterns in trace element signatures (Figure 1). Sampling sites represented

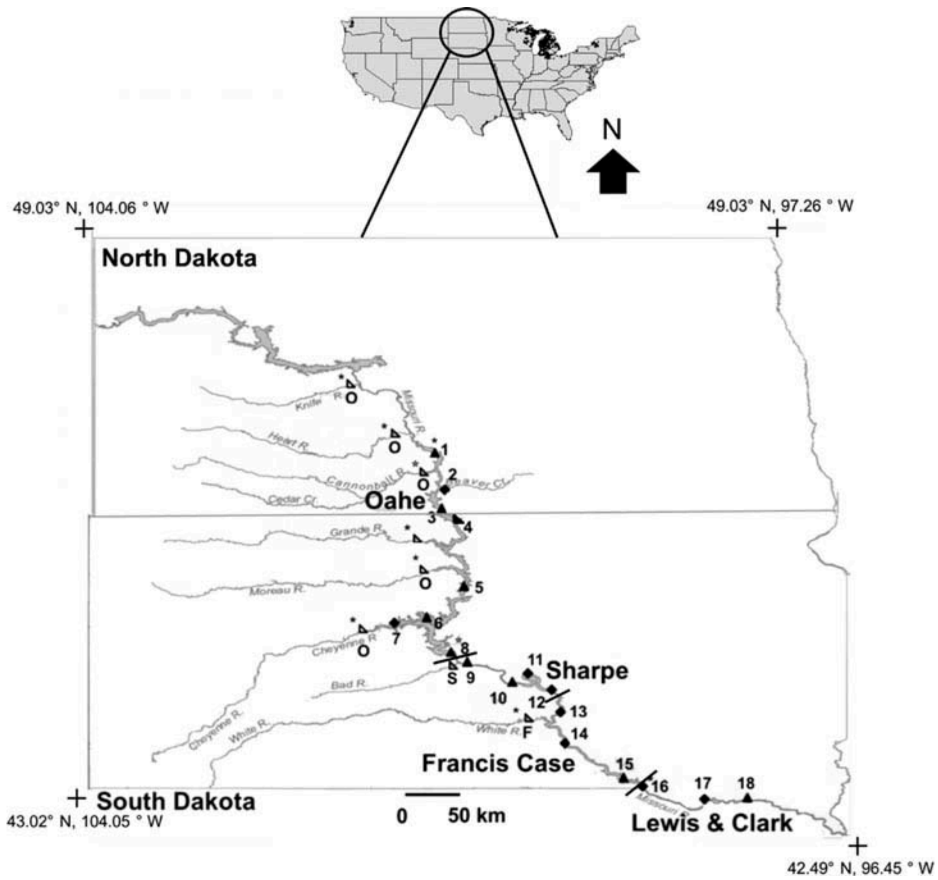

FIGURE 1. Water chemistry and Walleye sampling locations in Missouri River reservoirs, North Dakota and South Dakota. Shapes denote locations where Walleyes of different ages were collected: age 0 (right-angle triangles), adult (upright triangles), both ages (diamonds). Water samples were collected at all age-0 and combined age-0 and adult sites in 2012 and at sites marked with an asterisk (*) by the U.S. Geological Survey from 1982 to 1989. Tributaries and main-stem–embayment sites are represented by unfilled and filled shapes, respectively. Reservoirs associated with tributaries are denoted by O (Lake Oahe), S (Lake Sharpe), and F (Lake Francis Case) and are separated by solid lines. Numbers designate main-stem or embayment sites: (1) Garrison Dam, (2) Beaver Bay, (3) Fort Yates, (4) West Pollock Bay, (5) West Whitlock Bay, (6) Bush's Landing, (7) Minneconjou Bay, (8) Oahe Dam, (9) Pierre, (10) Fort George, (11) West Bend Bay, (12) North Shore Bay, (13) Francis Case stilling basin, (14) Platte Creek Bay, (15) North Bay, (16) Lewis and Clark tailrace, (17) Lewis and Clark delta, (18) Gavins Point Dam.

known Walleye natal areas (South Dakota Game, Fish and Parks, unpublished data). A syringe filtration method for sampling in remote field locations (Shiller 2003) and used in previous otolith microchemistry studies (Zeigler and Whitledge 2010, 2011; Phelps et al. 2012) was employed. All water samples were collected in 250-mL, acid-washed, polyethylene bottles prerinsed with river water by researchers wearing nitrile gloves. Samples were filtered with an acid-washed syringe equipped with a Whatman Puradisc PP 0.45-μm filter into acid-washed polyethylene storage vials. Samples were stored in sealed coolers (i.e., no light penetration) before trace element analysis at the University of Southern Mississippi. There, samples were acidified with a solution containing 2% nitric acid and analyzed with high-resolution, inductively coupled plasma mass spectrometry (HR-ICPMS) using four calibration standards prepared from National Institute of Standards and Technology (NIST) standards run after every 10 samples (Clarke et al. 2007). The complete analytical protocol is described in Shiller (2003). Measured concentrations (μg/L) of Sr, Ba, and calcium (Ca) were subsequently converted to molar element: Ca ratios (mmol/mol).

Surficial and bedrock geology are temporally stable in Missouri River impoundments and presumably result in consistent water signatures over time (Bickford and Hannigan 2005). To confirm this, historical (1982–1989) Sr:Ca and Ba:Ca ratios were compared with current signatures to evaluate temporal patterns in water chemistry and assess the reliability of otolith microchemistry as an environmental history tool, particularly for Walleyes older than the duration of water sampling in this study (i.e., 2 years). Historical Sr, Ba, and Ca concentrations were obtained from the U.S. Geological Survey National Stream Water-Quality Monitoring Network for Region 10, which includes the North Dakota and South

Dakota portion of the Missouri River (Alexander et al. 1996). Historical spring (i.e., March–May) and summer (i.e., July–September) water samples (n = 2–4/site) were collected in seven tributaries and three main-stem locations in Lakes Oahe, Sharpe, and Francis Case also sampled in this study. Trace element concentrations were quantified using an ICPMS protocol analogous to the one employed in our study. Water samples were filtered and fixed in dilute acid solution, and flame-atomic absorption or solution-mode ICPMS was used to measure elemental concentrations, depending on the element and date of sampling (Alexander et al. 1996). Historical data were available over 5 years in tributaries (1983–1986, 1989) and main-stem locations (1982–1986).

Fish sampling.—In partnership with South Dakota Game, Fish and Parks (SDGFP), 63 age-0 Walleyes were collected during their first growing season in summer 2012 concurrently with water sampling in tributaries (n = 29 individuals, 2–5 per site), embayments (n = 28 individuals, 2–7 per site), and main-stem locations (n = 6 individuals, 2–8 per site) using nearshore electrofishing (pulsed DC, 60 pulses/s, 6–8 A; Figure 1). Total length of each fish was measured and ranged from 76 to 114 mm. A total of 228 adult Walleyes were collected in July–September 2013 in 18 embayment and main-stem locations (n = 10–18/site) distributed throughout Missouri River reservoirs using electrofishing and 46-m-long, experimental-mesh, gill nets (bar mesh, 15–51 mm). Although adult Walleyes are known to move between the upper and lower ends of Missouri River reservoirs and among impoundments (i.e., entrainment; Longhenry, personal communication), movements spanning the entire study area have not been documented and are likely rare, rendering the sampling protocol appropriate for addressing study objectives. Total length of each individual was recorded and ranged from 190 to 756 mm. Adults were age 2 to age 11 years, in which the majority (68.31%) were ages 2 or 3, nearly one-quarter (23.87%) were ages 4 or 5, and older age-classes were each represented by 1–8 individuals.

Otolith microchemistry.—Age-0 and adult Walleyes were sacrificed immediately after collection and stored on ice in site-specific plastic bags in sealed coolers until same-day otolith extraction in a laboratory. Left and right sagittal otoliths from each individual were removed using plastic forceps triple-washed in nitric acid (Campana et al. 2000; Brazner et al. 2004). The otolith with the most well-defined annuli was used for age estimation by three independent readers (correspondence > 90%: Quist et al. 2013). In preparation for trace element analysis, otoliths were triple-rinsed in ultrapure water, air-dried for a minimum of 24 h, and stored in acid-washed, 2-mL, polypropylene, microcentrifuge tubes (Zeigler and Whitledge 2010). After initial cleaning, adult otoliths were embedded in Epo-Fix epoxy and sectioned in the transverse plane using a low-speed Isomet diamond saw (Buehler, Lake Bluff, Illinois). Each section included the otolith core, and contamination was prevented by cleaning the saw blade with an unused, dry sheet of aluminum oxide lapping film (3-μm grit) after each cut. Age-0 otoliths were placed in thermoplastic cement and ground in the sagittal plane. All otoliths were sanded evenly with 3M wet or dry sandpaper (400 grit) until the core was at the sample surface so that natal signatures could be measured. Otoliths were then polished with aluminum oxide lapping film to create a smooth surface for ablation. Otoliths were then mounted on acid-washed petrographic slides (Donohoe and Zimmerman 2010), triple-sonicated in ultrapure water, and dried in a Class 100 laminar flow hood for 24 h.

Concentrations of the two trace elements, ^{88}Sr and ^{137}Ba, and ^{43}Ca were quantified with laser ablation ICPMS at the University of California–Davis Interdisciplinary Center for Inductively Coupled Plasma Mass Spectrometry. An Agilent Technologies 7500a quadrupole ICPMS coupled to a New Wave Research UP-213-nm laser with helium as the carrier gas was used for laser ablation. Laser parameters were 70% energy, 10-Hz pulse rate, 40-μm spot size, 50-s acquisition, and 25-s background. The U.S. Geological Survey synthetic glass standard GSE-1G was used as the calibration standard, and two additional reference standards (GSD-1G and MACS-3) were used as quality controls for verification of instrument accuracy and precision. Each standard was ablated in three to five locations after every four samples to adjust for possible instrument drift. Isotopic counts were converted to elemental concentrations (μg/g) after correction for gas blank, matrix, and drift effects using specialized computer software (i.e., Glitter 4.4; GEMOC CSIRO, Macquarie Research, Macquarie University, Sydney, Australia). Otolith elemental concentrations were well above mean limits of detection (0.01 for ^{88}Sr, 0.07 for ^{137}Ba), which were calculated as mean blank values plus three standard deviations (Wells et al. 2003). All water and otolith data were reported as element: Ca ratios (mmol/mol) as Ca is a pseudointernal standard (Bickford and Hannigan 2005; Ludsin et al. 2006; Whitledge et al. 2007).

All otoliths were ablated using spot analyses. For each spot, a 15-s laser warm-up time was followed by a 20-s dwell time, during which the sample was ablated. The integration time for all elements (0.01 s for ^{43}Ca, 0.05 s for ^{88}Sr and ^{137}Ba) was repeated throughout the 20-s dwell time. Following each ablation, there was a 95-s washout time. Natal origins of adult Walleyes were identified by ablating otolith cores and comparing Sr:Ca and Ba:Ca ratios to site-specific signatures established using age-0 otoliths (Ruttenberg et al. 2005), a process that required water and otolith signatures to be temporally matched. Water and otolith samples were generally collected at the same time in summer 2012, and signatures were temporally matched by ablating otoliths at terminal edges, which reflect environments recently occupied by the fish (Zeigler and Whitledge 2010, 2011). Hereafter these signatures are referred to as "mean terminal." When logistical sampling constraints precluded water–otolith synchronization, age-0 individuals were invariably collected after the water samples, which permitted laser ablation at nonterminal otolith locations to quantify "adjusted mean terminal" signatures that corresponded with the time of water sampling. Water and otolith chemistries were synchronized by enumerating the time span between water and age-0 Walleye sampling and ablating otoliths in an equivalent number of daily rings from otolith edges. Temporal matching of water and age-0 otolith chemistry ensured otolith signatures accurately represented known capture locations and were reliable for identifying adult natal origins (Zeigler and Whitledge 2010, 2011).

Statistical analysis.—Normality and homoscedasticity of water and otolith Sr:Ca and Ba:Ca were evaluated using Shapiro–Wilk and Levene's tests, respectively. Untransformed and $\log_{10}$-transformed summer water signatures were not normally distributed and had unequal variances. Thus, spatial patterns in historical (1982–1989) and current (2012) Sr:Ca and Ba:Ca were assessed using a Kruskal–Wallis (KW) test (Blair and Hicks 2012; Amano et al. 2013), a nonparametric alternative to one-way ANOVA. Historical data were separated by habitat type due to time span differences between tributaries and main-stem locations. Post hoc multiple comparisons were performed using a Tukey–Kramer–Nemenyi test, a nonparametric version of Tukey's honestly significant difference test (Pohlert 2014). Seasonal and annual patterns in historical tributary and main-stem signatures were assessed through examination of site × time (i.e., season, year) interactions using Friedman's two-way ANOVA by ranks, a nonparametric alternative to two-way ANOVA. Summer signatures were used for site × year interactions. Long-term patterns in summer Sr:Ca and Ba:Ca were evaluated using the Friedman's two-way ANOVA site × period (i.e., historical, current) interaction. Mean signatures and 95% CIs were also compared between periods. Terminal (i.e., mean terminal, adjusted mean terminal) otolith signatures from age-0 Walleyes were normal with equal variances for Sr:Ca but not for Ba:Ca, necessitating the use of both ANOVA and a KW test for assessing spatial patterns. Water–otolith relationships were evaluated with least-squares linear regression (Munro et al. 2005; Zeigler and Whitledge 2010; Phelps et al. 2012) using water and age-0 Walleye terminal otolith signatures from each site. Statistical significance for all analyses was set at $\alpha < 0.05$.

The accuracy with which age-0 Walleyes could be classified to known collection habitats (i.e., tributaries, embayments, main-stem locations) and individual sites based on terminal otolith Sr:Ca and Ba:Ca signatures was evaluated using k-sample nearest-neighbor discriminant analysis. This nonparametric method allows for reliable classification when otolith data do not meet parametric assumptions (Bickford and Hannigan 2005). It assigns age-0 individuals to natal sites to which the majority of their k nearest neighbors belong (Johnson 1998). The accuracy of different models (k = 2–8) was evaluated using a leave-one-out jackknife procedure, and the model with the lowest error rate (k = 2) was used to classify adults to natal sites using the known-origin data set (Ruttenberg et al. 2005). We assumed that adults could only hatch in reservoirs upstream (as opposed to downstream) from where they were collected or in the collection impoundment. Age-0 otolith Sr:Ca and Ba:Ca signatures were used to develop the discriminant model under the notion that they would represent site-specific ratios of capture locations, unlike signatures of mobile adults. Adult natal origins were summarized as percentage contributions from tributaries, embayments, and main-stem sites. All analyses were performed in program R version 3.1.3 (R Development Core Team 2015).

RESULTS

Water Chemistry

Historical tributary signatures were spatially variable (Table 1); Sr:Ca decreased and Ba:Ca increased along a north–south gradient in Missouri River reservoirs. Historical main-stem Sr:Ca and Ba:Ca signatures were spatially homogeneous and heterogeneous, respectively. Spatial variability was consistent over the historical period when Sr:Ca and Ba:Ca signatures were stable between seasons and among years in tributaries and main-stem sites (Table 2). Current signatures were also spatially variable (Table 1). Water Sr:Ca and Ba:Ca ratios were consistent between historical and current time periods in tributaries (Sr:Ca: χ^2 = 0.14, df = 1, P = 0.71; Ba:Ca: χ^2 = 3.57, df = 1, P = 0.06) and main-stem sites (Sr:Ca: χ^2 = 3.00, df = 1, P = 0.09; Ba:Ca: χ^2 = 0.33, df = 1, P = 0.56). All but two signatures (Ba:Ca in the Cheyenne and Heart rivers in Lake Oahe) had overlapping means and 95% CIs between time periods (Table 3).

Otolith Chemistry

Linear regressions between water and otolith chemistry were positive and proportional for Sr:Ca (r^2 = 0.71, P < 0.01; Figure 2a) and Ba:Ca (r^2 = 0.40, P < 0.01; Figure 2b).

TABLE 1. Results of Kruskal–Wallis ANOVA comparing Sr:Ca and Ba:Ca signatures from Missouri River water in historical (1982–1989) and current (2012) time periods. Historical signatures were separated by habitat type due to time span differences between tributary and main-stem data. N denotes number of sites. Historical data were obtained from the U.S. Geological Survey National Stream Water-Quality Monitoring Network, whereas current data were collected in this study.

Signature	Period	N	χ^2	df	P
Sr:Ca	Historical (tributary)	7	54.57	6	<0.01
	Historical (main stem)	3	3.14	2	0.21
	Current	17	134.07	16	<0.01
Ba:Ca	Historical (tributary)	7	38.24	6	<0.01
	Historical (main stem)	3	26.17	2	<0.01
	Current	17	134.30	16	<0.01

TABLE 2. Results of Friedman's two-way ANOVA by ranks comparing historical (1982–1989) Sr:Ca and Ba:Ca signatures from Missouri River water between seasons (spring and summer) and among years. Results of site × season and site × year interactions are reported. Signatures were separated by habitat type due to time span differences between tributary and main-stem data, all of which were obtained from the U.S. Geological Survey National Stream Water-Quality Monitoring Network.

Interaction	Signature	Type	χ^2	df	P
Season	Sr:Ca	Tributary	1.29	1	0.26
		Main stem	2.00	1	0.16
	Ba:Ca	Tributary	0.14	1	0.71
		Main stem	1.00	1	0.32
Year	Sr:Ca	Tributary	5.21	4	0.27
		Main stem	7.80	4	0.10
	Ba:Ca	Tributary	5.94	4	0.20
		Main stem	1.20	4	0.88

TABLE 3. Sr:Ca and Ba:Ca signatures (mean ± 95% CI) for seven Missouri River tributaries and three main-stem sites sampled historically (1982–1989) and in 2012 in this study. All but two signatures, denoted by an asterisk (*), overlapped between time periods.

Site	Signature	Historical	Current
	Tributary		
Cannonball River	Sr:Ca	6.22 ± 0.08	6.42 ± 0.14
	Ba:Ca	0.25 ± 0.03	0.20 ± 0.10
Cheyenne River	Sr:Ca	5.85 ± 0.35	5.98 ± 0.24
	Ba:Ca*	0.11 ± 0.02	0.06 ± 0.01
Grand River	Sr:Ca	6.52 ± 0.32	6.37 ± 0.01
	Ba:Ca	0.36 ± 0.10	0.36 ± 0.01
Heart River	Sr:Ca	6.29 ± 0.41	6.40 ± 0.01
	Ba:Ca*	0.34 ± 0.02	0.21 ± 0.01
Knife River	Sr:Ca	7.26 ± 0.27	7.12 ± 0.29
	Ba:Ca	0.27 ± 0.05	0.23 ± 0.01
Moreau River.	Sr:Ca	5.90 ± 0.15	5.78 ± 0.36
	Ba:Ca	0.15 ± 0.03	0.14 ± 0.01
White River	Sr:Ca	3.36 ± 0.17	3.33 ± 0.04
	Ba:Ca	0.32 ± 0.07	0.35 ± 0.01
	Main stem		
Garrison Dam	Sr:Ca	4.54 ± 0.08	4.76 ± 0.16
	Ba:Ca	0.29 ± 0.02	0.29 ± 0.03
Pierre	Sr:Ca	4.58 ± 0.13	4.72 ± 0.26
	Ba:Ca	0.22 ± 0.02	0.22 ± 0.04
Fort Randall Dam	Sr:Ca	4.59 ± 0.10	4.74 ± 0.18
	Ba:Ca	0.19 ± 0.01	0.19 ± 0.01

Site-specific age-0 signatures were heterogeneous for Sr:Ca (ANOVA: $F_{16,\ 41} = 54.25$, $P < 0.01$) and Ba:Ca (KW test: $\chi^2 = 55.39$, df = 16, $P < 0.01$) in accordance with spatial variability in Missouri River water chemistry. Age-0 Walleyes were reclassified with 82.0–93.0% accuracy to habitat types and 33.0–100.0% accuracy to individual sites based on terminal otolith Sr:Ca and Ba:Ca signatures (Table 4). All misclassified age-0 Walleyes (n = 16) were assigned to locations within the reservoir in which they were captured. Sites where misclassification occurred were the Cheyenne River (n = 1 individual) and Beaver Bay (n = 2), Minneconjou Bay (n = 1), West Pollock Bay (n = 2), and West Whitlock Bay (n = 2) in Lake Oahe; the Bad River (n = 2) in Lake Sharpe; and the White River (n = 1), Francis Case stilling basin (n = 2), North Bay (n = 2), and Platte Creek Bay (n = 1) in Lake Francis Case. One-half of these 16 individuals were correctly reclassified to natal habitat type (tributary or embayment). Reclassification accuracy based on habitat type was 100% in Lewis and Clark Lake, 92% in Lake Sharpe, 89% in Lake Oahe, and 73% in Lake Francis Case.

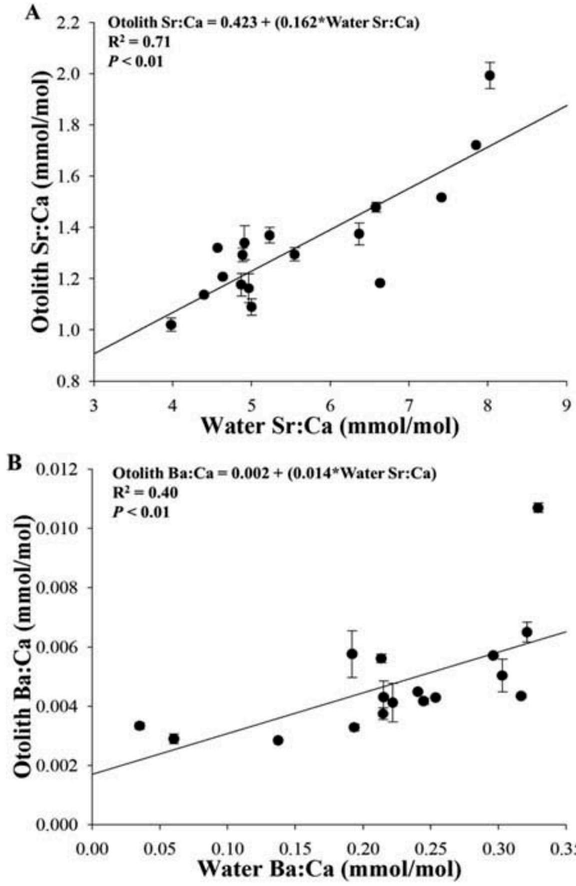

FIGURE 2. Linear regression of (**A**) Sr:Ca and (**B**) Ba:Ca signatures of the terminal otolith from age-0 Walleyes on equivalent ratios in water at collection sites in Lakes Oahe, Sharpe, and Francis Case and Lewis and Clark Lake. Fish and water sampling occurred in summer 2012. Error bars represent ±1 SE of the mean.

Natal Contribution

With high habitat- and site-specific reclassification accuracies, otolith signatures from age-0 Walleyes represented a

TABLE 4. Results of *k*-sample nearest-neighbor discriminant analysis with leave-one-out jackknife cross-validation for reclassifying age-0 Walleyes to natal sites based on otolith Sr:Ca and Ba:Ca signatures. Data include the number of individuals known to have come from habitat types and individual sites (Known), the number assigned to those locations (Assigned), and the percentage of individuals correctly classified to known locations (Accuracy). Signatures were measured at otolith locations synchronized with water sample collection to ensure reliable identification of natal origins. Lake Francis Case and Lewis and Clark Lake are denoted as FC and LC, respectively.

Natal origin	Known	Assigned	Accuracy
Site type			
Tributary	29	33	93.0
Embayment	28	24	82.0
Main stem	6	6	83.0
			Overall: 87.0
Site			
Bad River	4	4	50.0
Beaver Bay	2	1	50.0
Cannonball River	2	2	100.0
Cheyenne River	4	4	75.0
FC stilling basin	5	4	60.0
Grand River	5	8	80.0
Heart River	2	3	100.0
Knife River	2	2	100.0
LC delta	2	3	100.0
LC tailrace	7	5	60.0
Minneconjou Bay	4	4	75.0
Moreau River	2	2	100.0
North Shore Bay	8	7	75.0
Platte Creek Bay	4	3	75.0
West Bend Bay	2	2	100.0
West Pollock Bay	3	1	33.0
White River	5	8	86.0
			Overall: 75.0

reliable known-origin data set for identifying adult natal origins. Natal contributions of tributaries, including the Moreau River (38.5%, n = 37) and Cannonball River (18.8%, n = 18) in Lake Oahe, were large compared with combined main-stem and embayment sites (22.9%, n = 22; Table 5). The percentage of adults that hatched in tributaries decreased moving downstream from Lake Oahe (77.1%, n = 74) to Lake Sharpe (32.7%, n = 17), Lake Francis Case (25.0%, n = 10), and Lewis and Clark Clark Lake (22.5%, n = 9). Only 7.7% of Lake Sharpe individuals originated in that reservoir's single tributary (the Bad River), whereas 25.0% hatched in Lake Oahe tributaries (Table 5). The Bad and White rivers in Lake Francis Case contributed 25.0% of adults from that impoundment. Outside Lake Oahe, important natal sites included embayments (e.g., Beaver Bay, West Pollock Bay, Platte Creek Bay) and main-stem locations (e.g., North Shore Bay, West Bend Bay; Table 5). Notably, approximately two-thirds (67.3%) of Lake Sharpe adults hatched at North Shore Bay and West Bend Bay. Moreover, the Lewis and Clark Delta contributed 65.0% of adult Walleyes in that reservoir.

DISCUSSION

Prior to this study, Missouri River fisheries managers were unable to quantify habitat- and site-specific natal contributions because knowledge of Walleye reproduction was limited to anecdotal evidence of tributary and embayment spawning. Our results demonstrate the utility of otolith microchemistry for identifying Walleye natal origins and measuring natal contributions, supporting previous research on Walleye (Bickford and Hannigan 2005) and other freshwater species (Brazner et al. 2004; Zeigler and Whitledge 2010, 2011; Martin et al. 2012; Phelps et al. 2012). Otolith Sr:Ca and Ba:Ca ratios were spatially variable and temporally stable and thus served as reliable elemental signatures for characterizing Walleye provenance. Notably, water signatures were stable historically from 1982 to 1989, both between seasons and among years, and over a 30-year time span that exceeded the age of the oldest Walleye (age 11) captured in this study. Variability in water chemistry within and among reservoirs caused age-0 Walleye otolith signatures to have high habitat and site-specific reclassification accuracies, enabling reliable identification of adult natal origins. A large portion of adult Walleyes hatched in Lake Oahe tributaries, particularly the Moreau and Cannonball rivers, supporting anecdotal evidence and our hypothesis regarding the significance of riverine natal areas. Natal contribution was also high in the Lewis and Clark Delta, a refuge environment during floods and nonflood periods (Carlson 2015) where Walleye reproduction has been observed (Graeb et al. 2009) and high-quality spawning and rearing habitats promote species-rich fish communities (Kaemingk et al. 2007). To our knowledge, our research was only the third Walleye otolith microchemistry study and the first in the Missouri River. However, this technique will likely be effective in all systems with spatially variable, temporally stable water chemistry (Zeigler and Whitledge 2010, 2011; Gahagan et al. 2012) and thus has broad applicability for Walleye management.

Our research supports a diverse body of literature demonstrating the applicability of otolith microchemistry for fisheries management throughout the world (Casselman 1982; Whitledge et al. 2007; Allen et al. 2009; Rohtla et al. 2014). Our findings have important implications for Walleye management in Missouri River reservoirs and other lotic and lentic systems throughout the species' range. Our results indicate that fisheries managers can promote spatially extensive Walleye reproduction and maintain spawner density in locations with low natal contribution by focusing broodstock collection efforts in sites with high natal contribution (e.g., Moreau and Cannonball rivers, North Shore Bay, West Bend Bay) while ensuring broodstock remain genetically diverse.

TABLE 5. Overall and site-specific percent (number in parentheses) natal contributions of tributaries and main-stem or embayment locations to Walleye populations in Missouri River reservoirs where adults were collected (top row). No individuals were assigned to sites in reservoirs located downstream from collection impoundments.

Water body (associated reservoir)	Oahe	Sharpe	Francis Case	Lewis and Clark
Tributaries				
Overall	77.1 (74)	32.7 (17)	25.0 (10)	22.5 (9)
Cannonball River (Oahe)	18.8 (18)	7.7 (4)	0.0 (0)	12.5 (5)
Cheyenne River (Oahe)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
Grand River (Oahe)	5.2 (5)	1.9 (1)	0.0 (0)	2.5 (1)
Heart River (Oahe)	6.3 (6)	1.9 (1)	0.0 (0)	2.5 (1)
Knife River (Oahe)	8.3 (8)	5.8 (3)	0.0 (0)	0.0 (0)
Moreau River (Oahe)	38.5 (37)	7.7 (4)	0.0 (0)	5.0 (2)
Bad River (Sharpe)		7.7 (4)	7.5 (3)	0.0 (0)
White River (Francis Case)			17.5 (7)	0.0 (0)
Main-stem and embayment sites				
Overall	22.9 (22)	67.3 (35)	75.0 (30)	77.5 (31)
Beaver Bay (Oahe)	8.3 (8)	0.0 (0)	0.0 (0)	0.0 (0)
Minneconjou Bay (Oahe)	1.0 (1)	0.0 (0)	0.0 (0)	0.0 (0)
West Pollock Bay (Oahe)	6.3 (6)	0.0 (0)	0.0 (0)	0.0 (0)
West Whitlocks Bay (Oahe)	7.3 (7)	0.0 (0)	0.0 (0)	0.0 (0)
North Shore Bay (Sharpe)		32.7 (17)	12.5 (5)	10.0 (4)
West. Bend Bay (Sharpe)		34.6 (18)	10.0 (4)	2.5 (1)
Platte Creek Bay (Francis Case)			40.0 (16)	0.0 (0)
Stilling basin (Francis Case)			12.5 (5)	0.0 (0)
Delta (Lewis and Clark)				65.0 (26)

Otolith microchemistry results also suggest that tributaries and embayments with high natal contribution should be protected from sedimentation, shoreline erosion, damming, pollution, and other stressors to promote Walleye reproduction and riparian functions and services (e.g., nutrient cycling, flood control, sediment control).

Results from this study provide insight for future research in Missouri River reservoirs. First, Walleyes were not exclusively lake resident–river spawning types as main-stem spawning also occurred. Site-specific reclassification accuracies to main-stem locations were relatively low, hindering assessment of natal origins at these sites. Future researchers may improve reclassification in Missouri River impoundments and other lotic systems by using isotopic signatures (e.g., $\delta^{13}C$, $\delta^{18}O$, $\delta^{2}H$, ^{87}Sr:^{86}Sr; Zeigler and Whitledge 2010, 2011; Rohtla et al. 2014). These tracers may also enable researchers to quantify chemical variability within tributaries and embayments and evaluate natal origins and movements of Walleyes and other species at finer scales (e.g., tributary headwaters versus confluence). Moreover, researchers may use otolith microchemistry to relate Walleye year-class strength to environmental factors (e.g., discharge, prey availability) to inform management of water levels, prey populations, and other ecosystem components. These advancements would improve Walleye management by enhancing the applicability and relevance of otolith microchemistry for natural resource agencies.

In summary, otolith microchemistry is a precise, high-resolution technique for identifying Walleye natal origins and measuring habitat- and site-specific natal contributions. Our study illustrates the utility of this technique in Missouri River reservoirs and suggests it is broadly applicable in lotic and lentic systems with spatially variable, temporally stable water chemistry. Demonstrating that otoliths serve as natural tags for ascertaining provenance, our research provides an approach to advance Walleye management. Otolith microchemistry represents a novel environmental history tool with important implications for broodstock collection, habitat protection and restoration, and harvest regulations.

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