A needle in a haystack: strontium isotopes (^{87}Sr/^{86}Sr) in otoliths identify origin of largemouth bass from a large Southwest reservoir

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Abstract

Largemouth bass *Micropterus salmoides*, a popular warm water sport fish, is routinely stocked in reservoirs throughout the USA to augment wild populations. Evaluating if these supplementations are successful requires distinguishing hatchery-sourced fish from their wild counterparts. From 2011 to 2019, over 467 000 largemouth bass fingerlings were stocked from multiple hatchery sources into a large southwestern reservoir (Elephant Butte Reservoir, New Mexico, USA) to supplement the sport fish population. To identify hatchery-sourced largemouth bass, we measured strontium isotope ratios (^{87}Sr/^{86}Sr) and determined ages using otoliths and dorsal spines. Otolith analysis of 169 fish classified 92.9% ($n = 159$) to the reservoir with few fish of hatchery origin (2 from Arkansas, 1.2%, and 1 from Montana, 0.6%). While stocking over 467 000 fingerlings across 8 years appears to reflect negligible stocking success, it is likely that low and variable stocking densities (average 3.0, range 0.29–7.77 fish·ha^{-1}) contributed to the low stocking success in Elephant Butte Reservoir. Dorsal fin spines did not yield accurate age reconstructions and their ^{87}Sr/^{86}Sr values were affected by matrix interferences preventing source assignments.

Key words: ^{87}Sr/^{86}Sr, largemouth bass, stocking, retrospective age analysis, otoliths, dorsal spines

Introduction

Fish stock enhancement is a popular method for increasing the abundance of a target species, which involves the introduction of hatchery-reared fish. This approach is used to enhance the productivity of fisheries, restore degraded populations, and support recreational and commercial fishing activities (Welcomme and Bartley 1998; Molony et al. 2003). The introduction of hatchery-reared fish can have various impacts on existing wild populations, including genetic and ecological effects (Araki and Schmid 2010). Therefore, accurately identifying hatchery-reared fish is essential for assessing the impacts of stock enhancement on the wild population and making informed management decisions. To evaluate supplementation efforts, however, hatchery-reared individuals must be distinguished from wild or naturally spawned fish.

A variety of batch-marking techniques are available and include visible-implant elastomeric marks and injected coded-wire tags; however, these can result in tagging loss through time or increased susceptibility to stress and predation (Catalano et al. 2001; Hartman and Janney 2006). In addition, large numbers of fish must be marked to ensure a high probability of obtaining a sufficient size of tagged fish to assess the effect of stocking on wild fish populations. Biological tags such as parentage-based genetic assignment (Hargrove et al. 2022) are non-lethal, requiring a small amount of tissue; however, genetic analyses can be somewhat costly. Chemical marks of calcified structures from immersion baths include oxytetracycline (Hoffman and Bettoli 2005), calcein (Hill and Quesada 2010), and strontium chloride hexahydrate (Hobbs et al. 2012). While chemical marking is cost-effective, some methods have drawbacks such as incomplete or poor retention after marking (Hill and Quesada 2010) and the potential of fish mortality due to chemical exposure and handling (Hobbs et al. 2012).

Alternatively, hatchery and wild origin individuals can be distinguished based on the geochemical analyses of calcified structures that form throughout the life of a fish and incorporate the naturally occurring differences in the geochemical makeup of different watersheds (Campana 1999; Nelson et al. 2013; Willmes et al. 2016*a*; Sellheim et al. 2017). The ^{87}Sr/^{86}Sr isotope signal is passed from water into the fish exchanging in trace amounts for calcium in calcified structures such as otoliths reflecting a chronological record of geochemistry (Kalish 1989; Hegg et al. 2013; Coelho et al. 2017). For example, Volk et al. (2000) distinguished anadromous and freshwater resident Pacific salmonids using ^{87}Sr/^{86}Sr signatures from

primordial cores of otoliths. Others have used ^{87}Sr/^{86}Sr signatures from otoliths to assign natal origin in wild Chinook salmon *Oncorhynchus tshawytscha* (Barnett-Johnson et al. 2008; Brennan et al. 2015), steelhead *Oncorhynchus mykiss* (Watson 2016), American shad *Alosa sapidissima* (Walther et al. 2008), and walleye *Sander vitreus* (Carlson et al. 2016). Using ^{87}Sr/^{86}Sr signatures in otoliths, Radigan et al. (2018) demonstrated the importance of floodplain habitat for natal origin to a diverse group of sport fishes.

Largemouth bass *Micropterus salmoides* is a warmwater species that represents an important recreational fishery in the United States (USFWS 2018). While native to the Mississippi River basin and the Atlantic drainage (Fuller et al. 2021), the popular sport fish is stocked into reservoirs across the United States to enhance populations through supplementing year classes (Mesing et al. 2008). Water management in regions of high aridity, however, must balance irrigation and municipal demands with spring flows that results in water-level fluctuations that may not be suitable to largemouth bass, a species that relies on littoral areas for spawning and rearing of young. Annual fluctuations in Elephant Butte Reservoir, New Mexico, USA, are tied to hydrology throughout the upper Rio Grande basin in the Southwest, which is highly variable and subject to long periods of drought (USBOR 2009; Woodhouse et al. 2012) and a warming climate (Kunkel et al. 2013). The perception that fishing for largemouth bass is poor in Elephant Butte Reservoir has prompted supplemental stocking of hatchery-reared fingerlings (NMDGF 2016). From 2011 to 2019, a total of 467 321 largemouth bass fingerlings (8–91 mm) were stocked into the reservoir from multiple hatchery sources to supplement the sport fish population (E. Frey (personal communication, 2019)). Unfortunately, hatchery origin fish were not marked to facilitate stock identification, and to evaluate the success of these supplementations requires distinguishing stocked fish from their wild counterparts. Thus, our goal was to use ^{87}Sr/^{86}Sr ratios in the first annulus (i.e., primordial region) of otoliths from a largemouth bass population in Elephant Butte Reservoir to determine fish origin and assess if hatchery supplementations were successful.

Otolith extraction is lethal and often undesirable if fish removal results in negative perception by the public or if the fish species is of conservation concern. Non-lethal alternatives to otoliths include scales, fin spines, and fin rays, which can also provide valuable information for the retrospective analysis of life histories that include natal origin (Muhlfeld et al. 2005), migration (Allen et al. 2009; Sellheim et al. 2017), and habitat use (Allen et al. 2018). Similar to otoliths, these hard structures form over time and can be used for isotopic analysis (Willmes et al. 2016a; Sellheim et al. 2017; Loeppky et al. 2020). However, the calcium phosphate of spines and fin rays may not accurately reflect annual cycles in older fish (Buckmeier et al. 2002; Isermann et al. 2003, 2010; Blackwell et al. 2019) and analytical methods first need to be validated before they can be broadly applied. Thus, our secondary objective was to characterize ^{87}Sr/^{86}Sr ratios in dorsal spines from largemouth bass to determine if these structures serve as a suitable tool to non-lethally assess the success of the stocking program in the reservoir.

Fig. 1. Location of Elephant Butte Reservoir, Sierra County, New Mexico, USA and where largemouth bass *Micropterus salmoides* were collected 2016–2020 from three coves (Kettle Top, McRae Canyon, and The Jungles). New Mexico shapefile from RGIS (2019) and United States shapefile from Massicotte and Smith (2023). Map projection is geographical and map datum is WGS84.
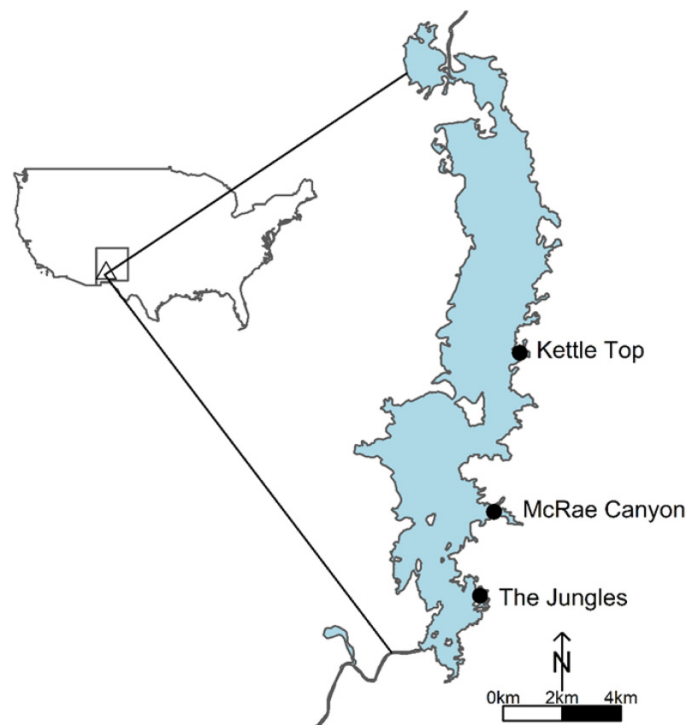
Materials and methods

Study area and fish collections for ^{87}Sr/^{86}Sr analysis

We conducted this study from October 2016 through October 2020 in Elephant Butte Reservoir (Sierra County, New Mexico, USA; Fig. 1). The reservoir drains approximately 75 000 km^2 and is the largest water body in New Mexico with a surface area averaging 14 800 ha and a total fill capacity of 2.5 km^3 (2 065 000 acre ft; USBOR 2009). The reservoir was constructed in the middle Rio Grande basin between 1911 and 1916 to manage irrigation needs, provide flood control, and generate electricity for southcentral New Mexico (USBOR 2009). The reservoir is considered one of the most important fishing destinations for largemouth bass anglers in New Mexico. However, population surveys indicate largemouth bass in the reservoir remains below the statewide relative abundance target of 20–40 fish·h^{-1} (NMDGF 2016). These data align with anglers' perception that the largemouth bass population in Elephant Butte Reservoir is inadequate, leading to the decision of supplementing the reservoir with hatchery-reared fingerlings from various hatchery sources.

In an earlier study, ^{87}Sr/^{86}Sr analysis from the primordial region of otoliths in the largemouth bass population in Elephant Butte Reservoir revealed 8.8% ($n = 3/34$) were hatchery-

Table 1. Origin, stocking date, approximate number, stocking density (fish·ha^{-1}), and mean length (mm) of fry and fingerling largemouth bass stocked in Elephant Butte Reservoir from hatchery sources in 2011–2019 (E. Frey, NMDGF).

Origin	Date	Number	Stocking density (fish·ha^{-1})	Mean length (mm)
Miles City, Montana	August 2011	68 000	3.64	41
Rock Lake, New Mexico	July 2012	5 383	0.29	64
Rock Lake, New Mexico	July 2012	6 479	0.36	91
Miles City, Montana	August 2015	36 900	1.31	53
Lonoke, Arkansas	March 2015	20 000	0.71	89
Miles City, Montana	August 2016	112 195	7.77	51
Miles City, Montana	September 2017	100 110	4.86	51
Rock Lake, New Mexico	June 2019	37 730	1.21	38

sourced fish (Vaisvil 2019). This prior knowledge reflected a good starting place for estimating the proportion of largemouth bass needed to calculate the sample size of fish that would ensure 95% confidence of obtaining a hatchery-sourced fish if present. Thus, we estimated 114 largemouth bass would be needed to ensure a level of precision of 0.05 with 95% confidence that our sample would contain a hatchery-sourced fish. A total of 146 largemouth bass were collected from Elephant Butte Reservoir to ensure an adequate sample size due to unforeseen issues such as broken or irregular otoliths. This precautionary measure allowed for a robust sample even if some otoliths were unable to be processed or were excluded during the analysis phase. We included the otoliths from 34 largemouth bass collected in 2016 to increase the total sample of our $^{87}Sr/^{86}Sr$ analysis to 180 largemouth bass. We collected these fish from three coves situated on the eastern shore of the reservoir because these areas contained suitable spawning substrate, submerged terrestrial vegetation, and coarse woody debris for largemouth bass (Vaisvil et al. 2022). Using a boat-mounted electrofishing unit (60 DC, 20%–40%, 5.2 m 5.0 GPP, Smith-Root, Vancouver, WA), we captured fish by targeting a range of sizes for each age class representative of a stocking year to increase the chances of capturing a hatchery fish stocked in 2011, 2012, 2015, 2016, 2017, and 2019 (Fig. S1). If fish were deemed the correct size class, we immediately euthanized the fish in a 200 mg·L^{-1} aqueous solution of tricaine methanesulfonate (MS-222; Tricaine-s, Western Chemical Inc., Ferndale, WA). Total length (±1.0 mm) and weight (±0.1 g) were recorded for each fish. We collected nine adult white bass *Morone crysops,* an abundant fish sourced only from Elephant Butte Reservoir, to obtain otoliths and dorsal spines as the reference values for $^{87}Sr/^{86}Sr$ signatures. These fish were captured and processed for otoliths and dorsal spines similarly to the largemouth bass.

To compare $^{87}Sr/^{86}Sr$ values of natal origin in Elephant Butte Reservoir with stocking origin of the commercial hatcheries, we obtained fingerling largemouth bass (35–168 mm) and water samples from each hatchery source that supplied fingerlings for stocking in Elephant Butte Reservoir between 2011 and 2019 (Table 1). Hatchery personnel collected, euthanized, and shipped 10–20 age-0 largemouth

bass from Miles City State Fish Hatchery, Montana (Montana Fish, Wildlife and Parks); Lonoke, Arkansas (F and L Anderson Farms, Inc.); and Rock Lake State Fish Hatchery, New Mexico (New Mexico Department of Game and Fish, Santa Rosa). The dorsal fin spines from these hatchery fish were too small (*i.e.,* less than 5 mm) to mount and analyze for $^{87}Sr/^{86}Sr$ chemistry.

Water $^{87}Sr/^{86}Sr$ analysis

We collected $^{87}Sr/^{86}Sr$ from surface water sampled using 50 mL polypropylene tubes from three coves within the general vicinity of the fish collections in Elephant Butte Reservoir. Using a 10 mL syringe, we filtered the water through a 0.2 μm pore filter (Whatman^{TM} Puradisk) and acidified the water sample with 1 M nitric acid. We supplied each hatchery source with the supplies to collect and ship the water to New Mexico State University. Immediately upon arrival, we filtered, acidified, and shipped the water samples to the University of California-Davis Interdisciplinary Center for Plasma Mass Spectrometry for $^{87}Sr/^{86}Sr$ analysis.

Strontium concentrations were determined using Agilent 8900 inductively coupled plasma mass spectrometer (ICP-MS, Agilent Technologies, Palo Alto, CA). An aliquot of each water sample was adjusted to obtain a mass of 1 μg of Sr. This volume was evaporated to dryness in an acid-leached PTFE (Teflon) vial on a hotplate, and Sr was isolated from all other aqueous constituents by selective ion exchange chromatography (Horwitz et al. 1992). Strontium isolates were reconstituted in 2% HNO$_3$ and introduced into the multicollector of the ICP-MS (Nu Plasma HR) using a desolvating nebulizer introduction system (Nu Instruments DSN-100, Wales, UK). All $^{87}Sr/^{86}Sr$ data were internally normalized by the measured $^{86}Sr/^{88}Sr$ ratio (assuming $^{86}Sr/^{88}Sr = 0.1194$). ^{85}Rubidium (Rb) was monitored to correct for ^{87}Rb if present, but all were well below the Rb correction threshold due to the selective ion exchange chromatography beforehand. Strontium isotopic ratios were monitored to estimate the Krypton (Kr) isotope ratios ($^{84}Kr/^{86}Kr$). ^{86}Kr was subtracted until the $^{84}Sr/^{88}Sr$ ratio equals the canonical value of 0.006755, while iterating the mass-bias correction. The procedural blank contributed <0.002% of total Sr processed per sample. Replicated analyses of NIST SRM 987 were conducted to normalize for instrument drift over the course of each daily session and for

Fig. 2. (A) Strontium isotope ratios (^{87}Sr/^{86}Sr) for moving average and spline with 95% confidence intervals for white bass otoliths sourced to Elephant Butte Reservoir. (B) ^{87}Sr/^{86}Sr moving average and spline with 95% confidence intervals in otoliths for hatchery-sourced largemouth bass from Arkansas. (C) ^{87}Sr/^{86}Sr moving average and spline with 95% confidence intervals in otoliths for hatchery-sourced largemouth bass from Montana. (D) ^{87}Sr/^{86}Sr moving average and spline with 95% confidence intervals in otoliths for hatchery-sourced largemouth bass from New Mexico. The upper, middle, lower, and bottom dashed lines represent the water ^{87}Sr/^{86}Sr signature for Elephant Butte Reservoir (NM(R)), Arkansas hatchery (AR), Montana hatchery (MT), and New Mexico hatchery (NM(H)), respectively.
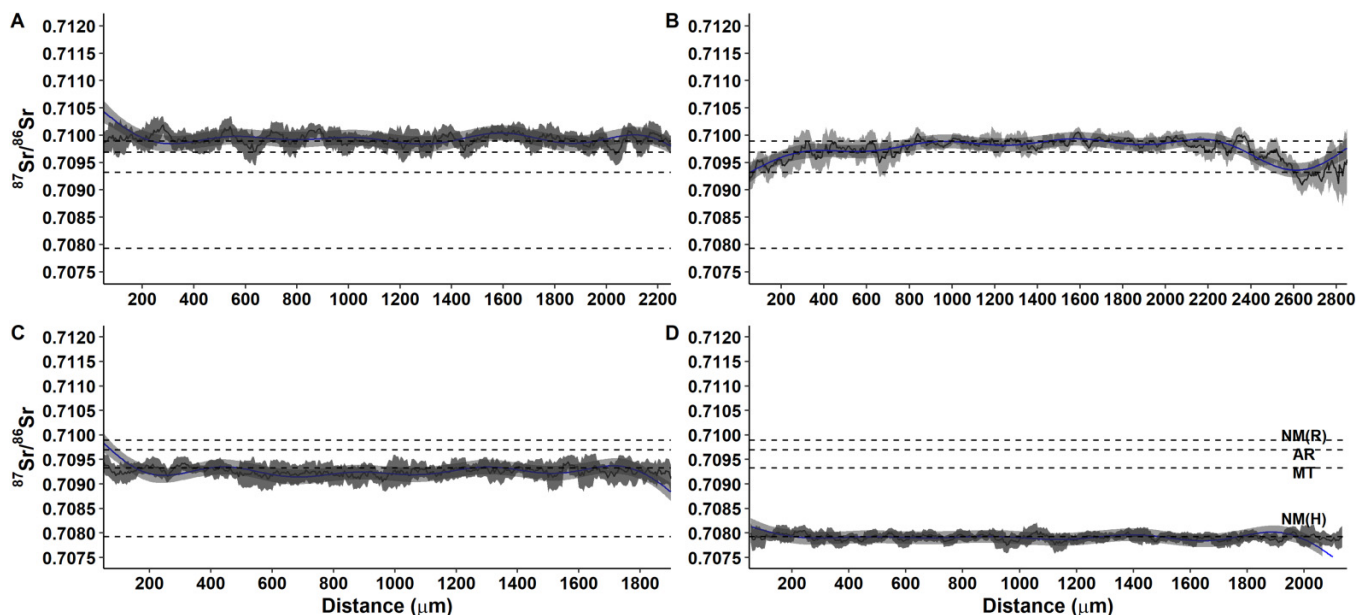
analytical artifacts among sessions. Replicate analyses of NIST SRM 987 yielded a mean ^{87}Sr/^{86}Sr value of 0.71025 ± 0.00002 ($n = 34$, ±2σ) and deemed in good agreement with the certified and accepted values (Faure and Mensing 2005).

Otolith and dorsal spine preparations for ^{87}Sr/^{86}Sr analysis

We removed sagittal otoliths from each fish and submerged the otolith in ultra-pure water in an ultrasonic water bath for 15 min to remove excess organic tissue. We embedded the left otolith, sulcus side facing upward, in Loctite® Clear Quick Set Epoxy (Henkel Corporation, Westlake, OH, USA). Using microscopy with transmitted light (100X, Leica Microsystems, Inc., DM4, Deerfield, IL, USA), we marked the primordial core of each otolith using a fine-point permanent marker. Using a low-speed saw (IsoMet, Buehler, Lake Bluff, IL, USA) fitted with a 12.7 cm wafering blade, we cut approximately 0.9 mm on either side of the marked core to create a longitudinal (sagittal) plane. We affixed the sagittal plane onto a glass slide using Crystalbond™ thermoplastic resin (Hobbs et al. 2010) and sanded the otoliths using an MTI Corporation UNIPOL 1210 grinding/polishing machine with 800 and 1200 grit sandpaper dampened with ultrapure water. We allowed the otoliths to dry for 48 h before affixing to a cover slip and mounting to petrographic slides using Crystalbond™ thermoplastic resin for ^{87}Sr/^{86}Sr analysis (Thorrold and Shuttleworth 2000; Hobbs et al. 2010).

We clipped the third (the longest) dorsal spine of each fish 1–2 mm distal to the articulation of the pterygiophores and

cleaned similarly to the otoliths. We set each spine proximal side up (vertically) in a thin layer of modeling clay and centered sections of plastic drinking straws over each spine. We filled the sections containing the dorsal spine with EpoxiCure 2 Epoxy (Buehler, Lake Bluff, IL) and allowed the epoxy to harden for 48 h. We performed two horizontal (transverse) cuts approximately 0.7 mm apart and 2–3 mm distal from the base of the spine using the low-speed saw fitted with a 12.7 cm wafering blade. Using the grinding/polishing machine, we sanded the sections with 800- and 1200-grit sandpaper dampened with ultrapure water. We dried the sections for 24 h before mounting to petrographic slides using Crystalbond™ thermoplastic resin for ^{87}Sr/^{86}Sr analysis.

Otolith and dorsal spine ^{87}Sr/^{86}Sr analysis

We measured strontium isotope ratios (^{87}Sr/^{86}Sr) at the University of California-Davis Interdisciplinary Center for Plasma Mass Spectrometry using an Nd/YAG 213 nm laser (New Wave Research UP213) coupled to a Nu Plasma HR MC-ICP-MS (Nu 032), following established methods (Willmes et al. 2018a). In brief, a laser beam 40 μm in diameter was traversed across the otolith from the dorsal edge above the sulcus, across the primordia, and to the ventral edge at 5 μm·s^{-1}, with the laser pulsing at 10 Hz frequency and 5–15 J·cm^{-2} photon output. We carried out data reduction using IsoFishR (Willmes et al. 2018b) and included normalization for mass bias, ^{87}Rb interference correction, and on-peak subtraction for ^{86}Kr. For each otolith, we applied a 5-point average to the

Fig. 3. Strontium isotope ratios ($^{87}Sr/^{86}Sr$) for source water (boxes) and otoliths (circles) from each source and overlaid onto box plots combining water and otoliths with the lower and upper bars corresponding to the 25th and 75th percentiles. Dark central band is the median. Water and otoliths of white bass were collected from Elephant Butte Reservoir in New Mexico (NM(R)). Water and largemouth bass otoliths were collected from a commercial hatchery in Arkansas (AR), and state hatcheries in Montana (MT) and New Mexico (NM(H)).
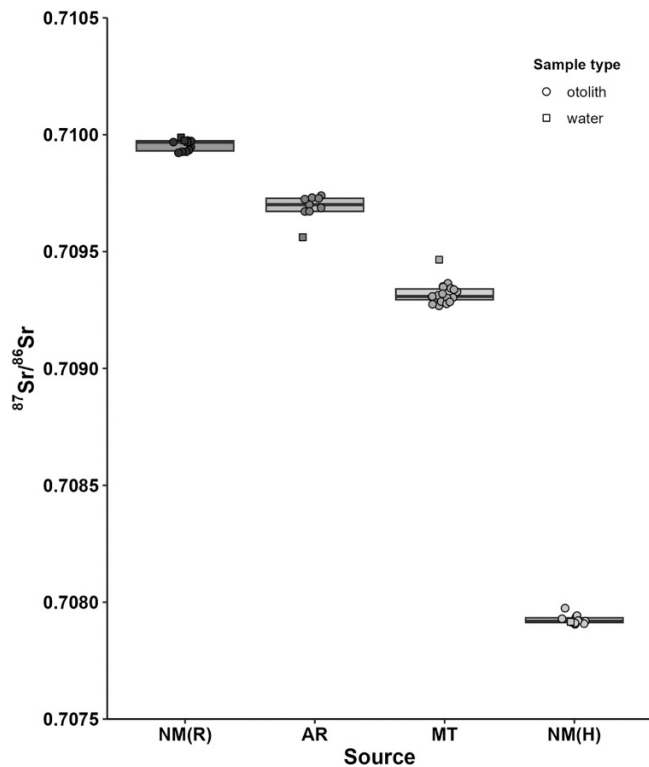
raw data collected by the mass spectrometer with an integration time of 0.2 s resulting in 1 data point per second. We removed outlier data based on a 20-point moving interquartile range (IQR) criterion. From the remaining data, we applied a thin plate spline ($k = 10$) to create a continuous, smoothed, and distance-resolved $^{87}Sr/^{86}Sr$ profile. For each otolith, the $^{87}Sr/^{86}Sr$ data were matched to the otolith images to identify the primordial region (reflecting natal origin) and the juvenile–adult region (representing time spent in the reservoir before capture). For each region, mean values and standard deviations of $^{87}Sr/^{86}Sr$ were calculated. Accuracy and reproducibility of the laser-ablation multi-collector inductively coupled plasma mass spectrometry (LA-MC-ICP-MS) were evaluated using in-house reference material consisting of a modern marine otolith from a white seabass *Atractoscion nobilis* collected offshore of Baja California. Replicate analyses yielded a mean $^{87}Sr/^{86}Sr$ value of 0.70915 ± 0.00013 ($n = 52, \pm 2\sigma$) in good agreement with the global average $^{87}Sr/^{86}Sr$ value of modern seawater of 0.70918 (McArthur et al. 2001).

Data reduction and natal origin assignments

We used the reference water samples and corresponding otoliths of known origins to create a $^{87}Sr/^{86}Sr$ baseline for each natal source. For white bass and water from Elephant Butte Reservoir and largemouth bass and water from the hatchery sources, we reduced the time-resolved $^{87}Sr/^{86}Sr$ data using IsoFishR (Willmes et al. 2018*b*) and graphed the data in R (R Core Team 2022). We compared $^{87}Sr/^{86}Sr$ signatures of otoliths to $^{87}Sr/^{86}Sr$ signatures for water from Elephant Butte Reservoir and the hatchery sources. The ablation distance for the otolith is represented by the *X*-axis on an interactive plot within IsoFishR (Fig. 2). To confirm the natal region of the otolith, we measured the transverse distance from the edge of the sample to the primordial region on the otolith using light microscopy ($40\times$) digital imaging software (LAS X; Leica Microsystems, Inc., Deerfield, IL). If the measured distance was within 50 μm of the distance identified in the IsoFishR figure, we assigned the otolith to the source corresponding to the $^{87}Sr/^{86}Sr$ signature identified from the source water. Examination of diagnostic plots (Sr voltage, $^{85}Rb/^{88}Sr$) led us to remove 11 fish from further data analyses as these showed large fluctuations in Sr signal. Upon close examination of the otoliths, we observed cracked or irregular otoliths resulting in the spurious $^{87}Sr/^{86}Sr$ values.

We then applied a linear discriminant function analysis (LDA), a supervised classification approach that maximizes variance among groups while minimizing variance within groups, using $^{87}Sr/^{86}Sr$ values within the primordial region of the otolith with the MASS package (Venables and Ripley 2002) in R (R Core Team 2022). We tested the LDA assumptions of normality using a Shapiro–Wilk's test and homogeneity of variance among groups using a Levene's test. Otoliths of known origin were split into a training (80%) and test (20%) datasets. The LDA model was constructed using only the training data and its performance evaluated on the test data using cross-validation. Samples with posterior probabilities <75% were classified as "unknown." Lastly, otoliths were aged by three expert reviewers (*see* retrospective age analyses of otoliths and dorsal fin spines) and compared to stocking dates. We then applied this LDA model to classify the natal origins from fish with unknown origins ($n = 169$). Some samples had low posterior probabilities and thus we assigned these as "unknown" because we could not assign these fish to either Elephant Butte Reservoir or a hatchery source.

Retrospective age analyses of otoliths and dorsal fin spines

After completing all $^{87}Sr/^{86}Sr$ analyses, we removed the otoliths and dorsal fin spines from the petrographic slides and attached each structure to a glass microscope slide to assign ages using a compound microscope ($40\times$) with transmitted light (Leica Microsystems, Inc., DM4, Deerfield, IL, USA). To reduce bias among three expert readers, age of otoliths and dorsal spines were estimated separately and independently and without knowledge of fish length or sex. To resolve the last annulus, the readers agreed that the hatch month of April/May would be used for largemouth bass in

Fig. 4. Strontium isotope ratios (^{87}Sr/^{86}Sr) for splines from otoliths ($n = 8$) of age-0 largemouth bass obtained from the Arkansas commercial hatchery. The dark horizontal line indicates approximate location of the core regions of the otoliths. The upper, middle, lower, and bottom dashed lines represent the water ^{87}Sr/^{86}Sr ratio for Elephant Butte Reservoir (NM(R)), Arkansas hatchery (AR), Montana hatchery (MT), and New Mexico hatchery (NM(H)), respectively.
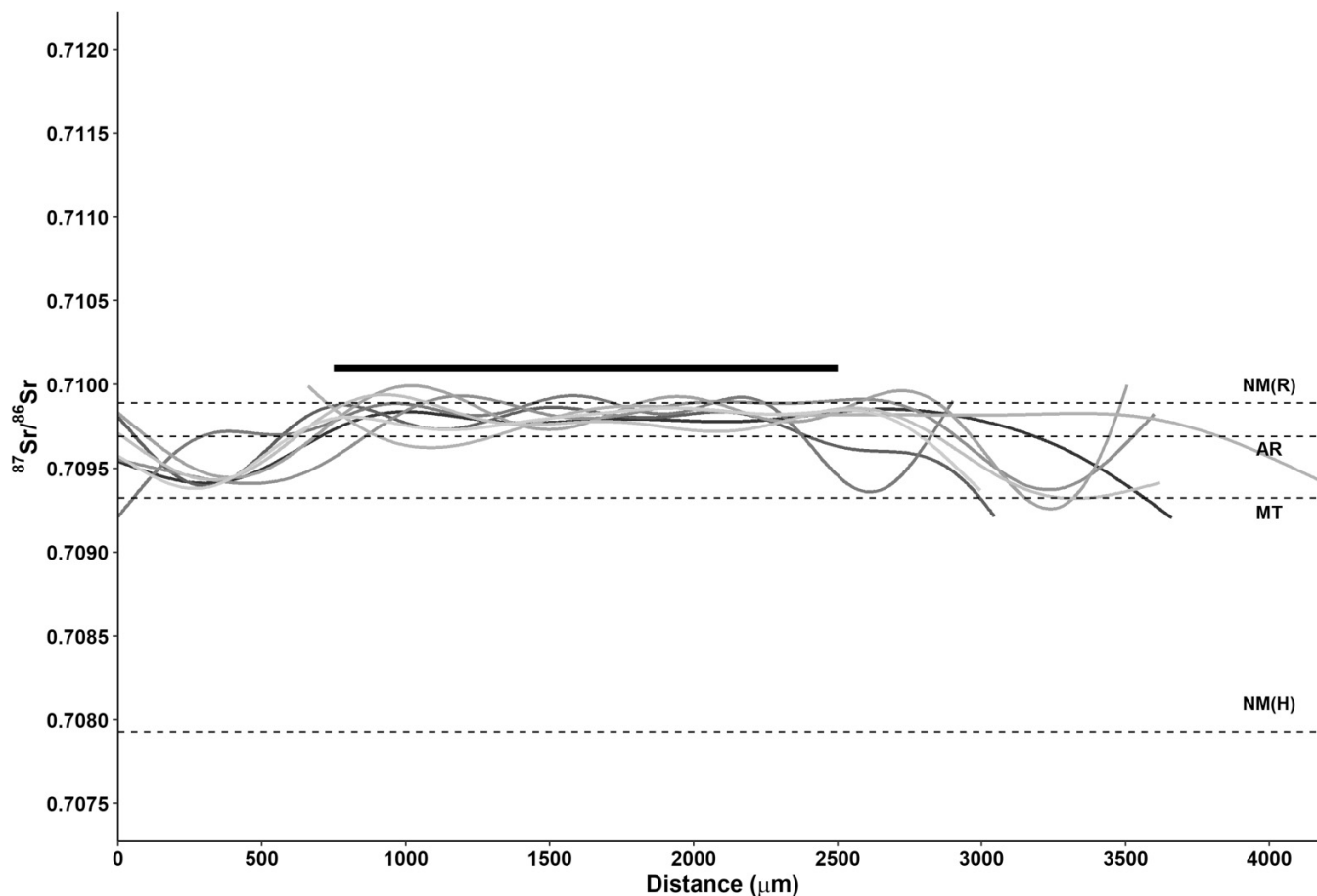
Elephant Butte Reservoir (Vaisvil et al. 2022). When assigned ages differed among readers, the readers consulted each other to develop a consensus of an estimated age. The coefficient of variation (CV; [SD/mean] × 100) was estimated as a measure of precision (Maceina et al. 2007) and is considered the most valuable estimate in assessing precision among readers and structures when the true age is unknown (Campana et al. 1995). Thus, we calculated the CV for otoliths and dorsal spines across the three readers. In addition, we were interested in learning if bias was evident among the three readers for both structures. Thus, we calculated the percentage when all three readers were in complete agreement, partial agreement when two of the three readers agree, and no agreement among the three readers (Isermann et al. 2010; Wegleitner and Isermann 2017). Lastly, we selected otolith ages to compare with the matching dorsal spines to assess the comparability of the two structures because sagittal otoliths often provide more accurate ageing data for *Micropterus* spp. (Maceina et al. 2007) than other hard parts of fish (*i.e.,* scales and spines; Maceina and Sammons 2006; Klein et al. 2017). If a fish was assigned as hatchery origin, then the estimated age using the otolith was compared to the stocking date. For these fish, the ^{87}Sr/^{86}Sr values through the primordial region
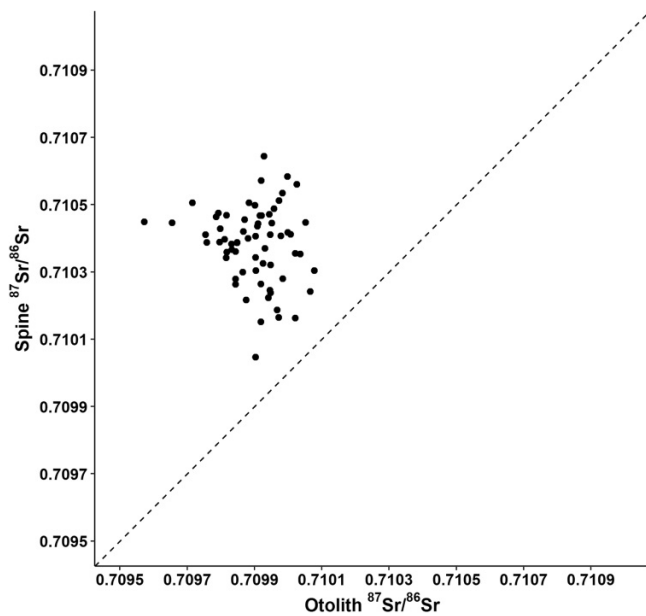
of the otolith had to corroborate with the ^{87}Sr/^{86}Sr values for the hatchery source.

Results

^{87}Sr/^{86}Sr assessment of otolith, spines, and water sources

The ^{87}Sr/^{86}Sr values of white bass otoliths (Elephant Butte Reservoir reference, average $\pm 2\sigma$, 0.70987 ± 0.000044, $n = 9$) were in agreement with the ^{87}Sr/^{86}Sr values of the source water (0.70998 ± 0.000010, $n = 3$) and were deemed a suitable reference of natal origin for Elephant Butte Reservoir (Fig. 3). The ^{87}Sr/^{86}Sr values of largemouth bass otoliths from Montana (0.70932 ± 0.000029, $n = 19$) were in good agreement with the source water (0.70947, $n = 1$). Similarly, the ^{87}Sr/^{86}Sr values of largemouth bass otoliths from New Mexico (0.70793 ± 0.000021, $n = 9$) were in good agreement with the source water (0.70792, $n = 1$). However, ^{87}Sr/^{86}Sr values of largemouth bass otoliths from the commercial Arkansas hatchery (0.70971 ± 0.000028, $n = 10$) differed from the source water (0.70956, $n = 1$), which is greater than an accuracy of ^{87}Sr/^{86}Sr $\pm 2\sigma$ standard deviation 0.0001. Upon

Fig. 5. Average strontium isotope values (^{87}Sr/^{86}Sr) of dorsal fin spines with ^{87}Sr/^{86}Sr values in matching otoliths from largemouth bass in Elephant Butte Reservoir. Diagonal line represents the 1:1 reference line for otolith and dorsal fin spine.
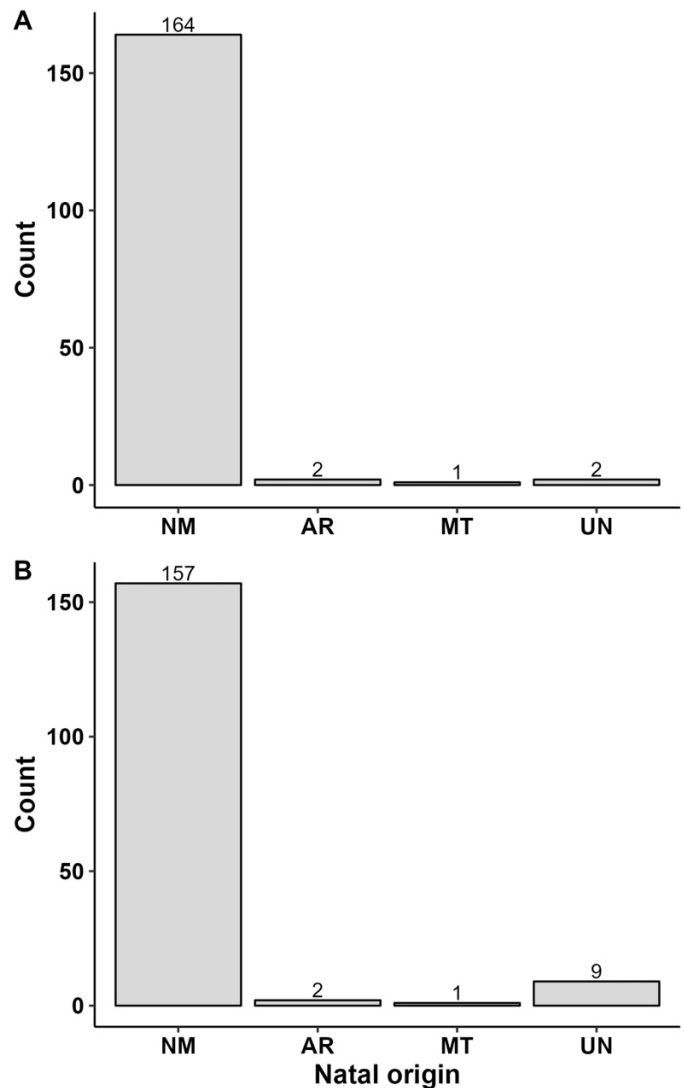

Fig. 6. (A) The initial linear discriminant function analysis classified 157 of 169 largemouth bass to Elephant Butte Reservoir (NM), 4 of 169 largemouth bass to the Arkansas commercial hatchery (AR), 1 of 169 largemouth bass to the state hatchery in Montana (MT), and 7 of 169 largemouth bass as unknown (UN). (B) After age analysis of the otoliths, final classifications remained 157 of 169 largemouth bass sourced to Elephant Butte Reservoir (NM), two largemouth bass were reclassified to unknown (UN) resulting in 9 unknown sources, and 1 largemouth bass remained sourced to the state hatchery in Montana (MT).

careful examination of the ^{87}Sr/^{86}Sr values in the reference otoliths from the Arkansas hatchery, we observed a shift in these values as we ablated from edge to core to edge (Fig. 4), indicating that these young fish were presumably moved between water sources. Despite the lower accuracy of the Arkansas hatchery source, the LDA model designated all sources as a relatively high classification success of 93% (Kappa = 91%, CI = 68%–99%) on the test data.

The ^{87}Sr/^{86}Sr values in the dorsal fin spines of white bass (Elephant Butte Reservoir reference, average $\pm 2\sigma$ standard deviation, 0.71046 $\pm$ 0.000015, $n = 11$) were not in agreement with the ^{87}Sr/^{86}Sr signatures for Elephant Butte Reservoir source water (0.70998 $\pm$ 0.000010, $n = 3$), which is greater than an accuracy of ^{87}Sr/^{86}Sr $\pm 2\sigma$ standard deviation of 0.0001. Similarly, when we compared the average ^{87}Sr/^{86}Sr value of the inner annulus in the dorsal fin spine with the average ^{87}Sr/^{86}Sr value of the otolith from the same fish, none of the ^{87}Sr/^{86}Sr values for the dorsal fin spine and otolith matched (Fig. 5).

^{87}Sr/^{86}Sr analysis of natal origin

Of the 169 unknown ^{87}Sr/^{86}Sr signatures from largemouth bass, our initial analysis assigned natal origins to Elephant Butte Reservoir ($n = 157$), the commercial hatchery of Arkansas ($n = 4$), and the state hatchery from Montana ($n = 1$), while the remainder were categorized as unknown ($n = 7$; Fig. 6A). Age assignments based on otoliths showed that only two fish (1.18%) had the correct age at stocking for the Arkansas hatchery source and one fish (0.59%) to the Montana hatchery (Fig. 6B). The core regions of these otoliths

clearly matched the Arkansas (Fig. S2) and Montana source (Fig. S3). The ages of the remaining nine fish (5.33%) did not match with the timing of the stocking records and the natal region of the otoliths could not be distinguished from Elephant Butte Reservoir (Fig. S4). The remaining 157 fish (92.9%) originated from Elephant Butte Reservoir (Fig. 6B). In these fish, the natal region of the otoliths matched the reservoir (*see* example in Fig. S4).

Fig. 7. Agreement between estimated ages of otoliths and dorsal fin spines ($n = 56$) of individual largemouth bass from Elephant Butte Reservoir, New Mexico. Dashed diagonal line is the 1:1 agreement in matched age structures.
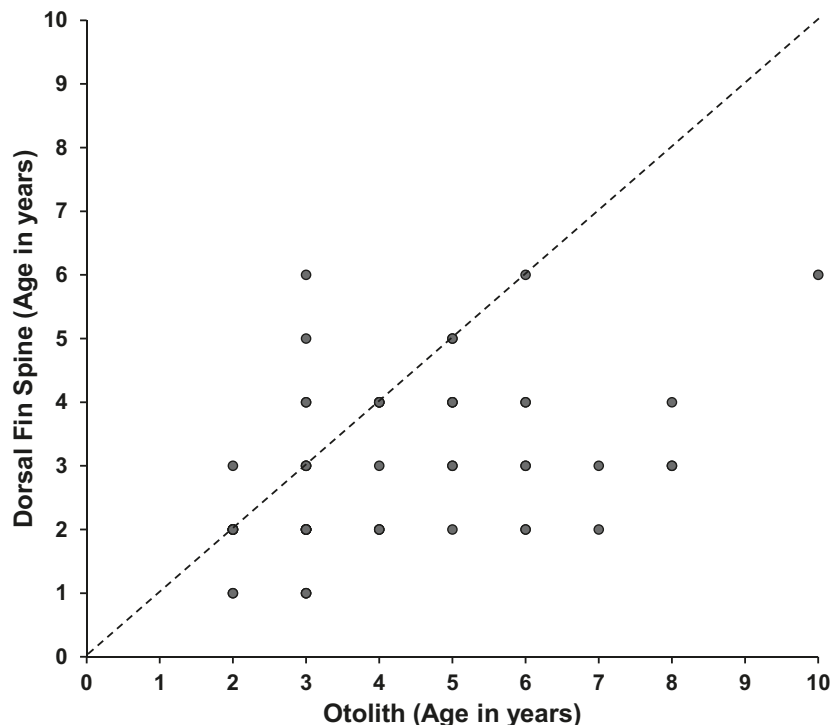
Retrospective age assignment between matched otoliths and dorsal spines

The average CV for otoliths and dorsal spines was 11.72% ($\pm$1.797 standard error) and 15.63% ($\pm$2.889), respectively. While complete agreement was lower among the three readers for otoliths (41.1%, $n = 23$) than for dorsal spines (46.4%, $n = 26$), there were fewer otoliths (7.1%, $n = 4$) than dorsal spines (14.3%, $n = 8$) in which all three readers did not agree on. When we selected the estimated ages for otoliths as the standard to compare with estimated ages of dorsal spines, we underestimated the ages in spines by an average of -1.16 (Fig. 7). Using light microscopy (100$\times$), closer examination of the dorsal fin spines in largemouth bass collected from Elephant Butte Reservoir revealed the first annulus was partially eroded for most fish age 2+ or greater. To assess if we missed the first annulus in our initial sectioning, we performed additional transverse cuts approximately 0.7 mm apart and 5–7 mm distal from the previous transverse cut and confirmed the first annulus was partially eroded or missing distally.

Discussion

We demonstrated that otolith ^{87}Sr/^{86}Sr values in combination with retrospective age analysis using otoliths identified hatchery-sourced fish from a largemouth bass population in large southwestern reservoir. By targeting specific size classes in the field collections, we obtained the appropriate age classes of largemouth bass that would likely reflect prior stocking events. From a relatively large sample of 169 largemouth bass, we identified three (1.78%) hatchery-sourced fish.

In addition, our analysis identified nine unknown-sourced fish (5.33%) with retrospective ages that did not match the timing of stocking events. These fish of known and unknown sources accounted for less than 7.1% of the total sample. While stocking over 467 000 fingerlings across 8 years appears to reflect negligible stocking success, it is likely that low and variable stocking densities (average 3.0, range 0.29–7.77 fish·ha^{-1}) contributed to the low stocking success in Elephant Butte Reservoir. Stocking recommendations for managing large oligotrophic reservoirs such as Elephant Butte (14 800 ha) are not available, but recommendations exist for small ponds and impoundments (*i.e.,* 125 fish·ha^{-1}; Wright and Kraft 2012), which would be cost-prohibitive and likely result in density effects to the fish community.

When compared to native largemouth bass, fewer stocked fish survive to adults and their contributions to the populations are low (Buynak and Mitchell 1999; Diana and Wahl 2008). In Oklahoma reservoirs, stocked largemouth bass were observed in the population for 3 years but declined thereafter (Boxrucker 1986). Hatchery-reared largemouth bass were absent 20 weeks post-stocking in a Texas–Louisiana reservoir (Ashe et al. 2016). A few exceptions include largemouth bass recruited into the population of Taylorsville Lake, Kentucky when stocked at 4.0–11.3 fish·ha^{-1} (Buynak and Mitchell 1999). Notably, the stocking densities in Taylorsville Lake were similar to the densities stocked into Elephant Butte Reservoir (0.29–7.77 fish·ha^{-1}). However, the largemouth bass stocked in Taylorsville Lake were larger (greater than 107 mm) than the fingerlings stocked in Elephant Butte Reservoir (8–89 mm). Buynak and Mitchell (1999) point to the

success of larger sized fish bypassing a recruitment bottle-neck. Stocking medium-sized (75–100 mm) fingerling large-mouth bass could be cost-effective because growth, survival, and prey availability would increase (Diana and Wahl 2009). Survival through winter of fingerling largemouth bass was identified as a benchmark for recruitment (Raibley et al. 1997; Buynak and Mitchell 1998), which is essential for main-taining year class strength. Dynamic abiotic conditions re-lated to water-level changes, common in Elephant Butte Reservoir (Vaisvil et al. 2022), can also affect the strength in year classes of largemouth bass (Sammons et al. 1999; Ozen and Noble 2005). It is noteworthy that two of the three hatch-ery origin fish were transported to various areas with pre-sumed suitable habitat, while other stockings occurred at one location (E. Mammoser, personal communication 2017).

We were unable to validate the dorsal spine as a non-lethal tool to determine natal origin in Largemouth Bass. Our find-ings indicate that the margins of the lumen of the dorsal fin spine contained remnants of the vascularized tissue, which replaces the calcium phosphate matrix of the first annulus (closest to the lumen of the fin spine), essentially erasing the natal record of fish with ages greater than or equal to one, precluding determining natal origin. There is no mention in the microchemistry literature of a blood vessel impinging on the first annulus; however, ageing studies of channel catfish *Ictalurus punctatus* (Buckmeier et al. 2002), walleye (Kocovsky and Carline 2000; Isermann et al. 2003), black crappie *Pomoxis nigromaculatus* (Isermann et al. 2010), and common carp *Cyprinus carpio* (Watkins 2015) identified erosion of the first annu-lus likely to result in spurious age information.

We observed dorsal fin spines exhibited higher average $^{87}Sr/^{86}Sr$ values when compared to $^{87}Sr/^{86}Sr$ in otoliths of the same fish. While Willmes et al. (2016a) presented dorsal fin spines and scales of walleye as viable alternatives to otoliths, we were unable to validate dorsal fin spines in largemouth bass using the same methodology. Additional work is needed to resolve the discrepancy between the biological apatite of the fin spine and aragonite of the otolith in these fish. Despite retuning the instrument for reduced oxide levels to account for the polyatomic interference resulting from the combina-tion of two or more isotopes of different elements ($^{40}Ar^{31}P^{16}O$ vs $^{40}Ca^{31}P^{16}O$) on mass 87 of Sr (Willmes et al. 2016b), the issue of higher $^{87}Sr/^{86}Sr$ values in the biological apatite of spines versus aragonite of otoliths persisted. Lastly, we recommend verification of the presence of the first annulus in fin spines to save time and resources associated with mass spectrome-try. Although lethal, otoliths are well-documented timekeep-ers of fish life histories and LA-MC-ICP-MS is a well-developed methodology to assess natal origin in fish.

While LA-MC-ICP-MS is a powerful analytical tool that en-ables highly sensitive elemental and isotopic analysis, there are assumptions associated with the geochemical origins of the samples that must be met. Notably, the otolith $^{87}Sr/^{86}Sr$ value from the Arkansas commercial hatchery (0.70971) was nearly indistinguishable from the $^{87}Sr/^{86}Sr$ signature of Ele-phant Butte Reservoir (0.70987). In addition, we noted incon-sistent $^{87}Sr/^{86}Sr$ patterns in the reference fish obtained from the Arkansas hatchery, reflecting that the largemouth bass were likely held in multiple water sources throughout their early life stages. This would explain the irregular $^{87}Sr/^{86}Sr$ profile between the otoliths and $^{87}Sr/^{86}Sr$ in the hatchery wa-ter source, which made it difficult to distinguish between the Arkansas hatchery source and Elephant Butte Reservoir.

Lastly, the stocked fish from the Arkansas hatchery were larger (89 mm) than the average stocking size of fingerlings from other hatchery sources (55.6 mm, range 38–91 mm). The overall larger size and early stocking in spring (March) of the Arkansas fingerling into Elephant Butte Reservoir may have resulted in the stocking of an older age class (1+).

Summary and recommendations

From 2011 to 2019, over 467 000 largemouth bass fry and fingerlings were stocked from multiple hatchery sources at relatively low stocking densities (0.29–7.77 fish·ha^{-1}) into a large southwestern reservoir to supplement the sport fish population. Of the 169 largemouth bass analyzed for $^{87}Sr/^{86}Sr$, we confirmed three fish from hatchery sources. While this appears to be a proverbial needle in a haystack approach, we targeted specific size classes to capture prior stocking events. When $^{87}Sr/^{86}Sr$ values of stocking origin dif-fer from the targeted waterbody and timing of the stock-ings is known, one can successfully use $^{87}Sr/^{86}Sr$ analysis and retrospective analysis of age in otoliths to determine natal origin. In combination with other techniques such as en-riched stable isotope marking prior to stocking (e.g., Munro et al. 2008), hatchery-sourced fish would be more easily dis-tinguished from wild fish. Additionally, future natal origin assignment models could likely be improved by the inclusion of trace elemental analyses (i.e., Sr/Ca, Ba/Ca) to differentiate among potential sources.

The dorsal fin spine was not a viable alternative for ret-rospective age analysis and thus non-lethal reconstruction of natal origin in largemouth bass. Additional work is needed to reconcile dorsal spine chemistry with otolith chemistry and to verify erosion of the first annulus of dorsal fin spines in the species and other managed populations throughout the US. Until then, the otolith and thus lethal removal of this popular sport fish will continue to be the standard for reconstructing natal origin of largemouth bass using $^{87}Sr/^{86}Sr$.

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Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

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