

# Life-history variation of two inland salmonids revealed through otolith microchemistry analysis

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**Abstract:** Increasingly, otolith microchemistry analysis is used as a tool to trace fish migrations, especially migrations of diadromous fishes. Yet, few studies have used otolith microchemistry to trace migrations in small inland watersheds, leaving major knowledge gaps in our understanding of inland fish spatial ecology. Here, we evaluate the use of tributary habitat for spawning and describe and compare fluvial brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) natal origin distribution, time spent in natal streams, and spawning site fidelity. 63% of rainbow trout and 57% of brown trout migrated after hatching. Brown trout showed greater variation in time spent in natal tributaries, suggesting that individuals are temporally distributing risk among offspring. By contrast, rainbow trout showed greater variation in natal origin, suggesting that individuals are spatially distributing risk among offspring. Our results indicate there is high inter- and intraspecific migration variation in inland salmonid populations, which may be linked to access to a mosaic of spawning and rearing habitat types.

**Résumé :** L'analyse de la microchimie des otolites est de plus en plus utilisée pour retracer les migrations de poissons, en particulier celles de poissons diadromes. Peu d'études ont toutefois utilisé la microchimie des otolites pour retracer les migrations dans de petits bassins versants intérieurs, de sorte que d'importantes lacunes persistent dans la compréhension de l'écologie spatiale des poissons d'eaux intérieures. Nous évaluons l'utilisation d'habitats d'affluents pour le frai et décrivons et comparons la répartition des origines natales, le temps passé dans le cours d'eau natal et la fidélité au site de frai de truites arc-en-ciel (*Oncorhynchus mykiss*) et de truites brunes (*Salmo trutta*) fluviales. En tout, 63 % des truites arc-en-ciel et 57 % des truites brunes migraient après l'éclosion. Les truites brunes présentaient une plus grande variation du temps passé dans l'affluent natal, donnant à penser que les individus répartissent le risque dans le temps parmi la progéniture. Les truites arc-en-ciel présentaient quant à elles une plus grande variation de l'origine natale, donnant à penser que les individus répartissent le risque dans l'espace parmi la progéniture. Nos résultats indiquent qu'il y a une grande variation inter- et intraspécifique des migrations chez les populations de salmonidés en eaux intérieures, qui pourrait être reliée à l'accès à une mosaïque de types d'habitats de frai et d'élevage. [Traduit par la Rédaction]

## Introduction

Biological diversity is expressed throughout the ecological hierarchy and plays a key role in maintaining ecosystem resiliency (see Helfman 2007; Elmqvist et al. 2003; Figge 2004). For example, a diverse grouping of species allows ecosystem functions to remain intact under a wide range of environmental conditions because different species promote similar ecosystem functions under different environmental conditions (Isbell et al. 2011). Similarly, life-history diversity can buffer populations against stochastic events by spreading risk and production over large geographic areas or across cohorts in the population, stabilizing population productivity and community structure (Waples et al. 2009; Greene et al. 2010, Moore et al. 2014).

In migratory fish populations, life-history diversity, and thus resiliency, is intimately connected with migration diversity because individuals migrate to satisfy physiological requirements, such as reproduction and feeding (Gross et al. 1988; Schmetterling 2001). For example, Schindler et al. (2010) found the migration diversity expressed by Bristol Bay sockeye salmon (*Oncorhynchus nerka*) decreased the annual variability in salmon return by 2.2 times and temporally extended the availability of nutrient-rich salmon carcasses to scavengers and predators by at least 1.5 months, ultimately

stabilizing terrestrial and aquatic ecosystems alike. Because population resiliency of migratory fish is tightly linked to migration diversity, identifying and preserving remaining migration variants may be essential for successful conservation of migratory fish populations (Waldman et al. 2016).

Technological advancements in otolith microchemistry analysis have given researchers the tools to identify migration variants (Barnett-Johnson et al. 2005). By analyzing chemical and isotopic concentrations longitudinally along otoliths, researchers can reconstruct the environmental history of fishes during all life stages and over large geographic areas (Hamann and Kennedy 2012; Muhlfeld et al. 2012; Brennan et al. 2015a). Since their development, otolith microchemistry techniques have been extensively used to study the migration diversity of anadromous salmonids (e.g., Outridge et al. 2002; Bacon et al. 2004; Volk et al. 2010; Hodge et al. 2016). Yet fewer studies have applied these techniques to inland salmonids (Wells et al. 2003; Muhlfeld et al. 2012; Percy and Miller 2018). Therefore, substantial knowledge gaps remain in our understanding of the migration diversity of inland salmonids.

Strontium isotope ratios ( $^{87}\text{Sr}/^{86}\text{Sr}$ ) are one of the more useful environmental signatures for reconstructing migration histories of freshwater fishes (Bacon et al. 2004; Gibson-Reinemer et al.

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2009).  $^{87}\text{Sr}/^{86}\text{Sr}$  incorporated into otoliths are tightly correlated with  $^{87}\text{Sr}/^{86}\text{Sr}$  measured in ambient fresh waters (Kennedy et al. 2000; Barnett-Johnson et al. 2008; Walther and Thorrold 2008; Muhlfeld et al. 2012). As a result, otolith  $^{87}\text{Sr}/^{86}\text{Sr}$  reflects the ambient water  $^{87}\text{Sr}/^{86}\text{Sr}$  the fish is inhabiting (Kennedy et al. 2000; Wolff et al. 2012). Additionally, large variation in ambient water  $^{87}\text{Sr}/^{86}\text{Sr}$  can exist throughout a stream network because  $^{87}\text{Sr}/^{86}\text{Sr}$  in fresh waters reflects the underlying watershed geology, with rock type, age, and weathering rates leading to variation in  $^{87}\text{Sr}/^{86}\text{Sr}$  (Bataille and Bowen 2012; Bataille et al. 2014).

We build on existing approaches of otolith microchemistry to quantify and compare the migration diversity of two inland salmonid species, rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*), residing in the Upper North Platte River (UNPR). Identifying the migration variants of rainbow and brown trout, within the same watershed, provided a distinct opportunity to compare the migration diversity expressed by two species that differ in a fundamental life-history trait: their timing of spawning. Rainbow trout are spring spawners and brown trout are fall spawners. Our specific research objectives were (i) evaluate the proportion of each population that are born in UNPR tributaries and migrate to the UNPR, hereinafter referred to as migrants, and (ii) for the proportion of each population that are migrants, evaluate the diversity of natal tributaries used, length of time spent in natal tributaries, and whether tributary use is consistent across years (e.g., straying). Additionally, we discuss the mechanisms that may support the observed migration diversity.

## Methods

### Site description

The North Platte River begins at the confluence of Grizzly and Little Grizzly creeks near Walden, Colorado, USA, then flows north to the Colorado–Wyoming state line, where it continues for 191 free-flowing river kilometres until it reaches Seminoe Reservoir. The headwaters of the North Platte River drain two mountain ranges, the Sierra Madre and Medicine Bow mountains. These ranges are geologically similar and contain a major shear zone, the Cheyenne belt, which separates the oldest Archean rocks to the north from the younger igneous and metamorphic rocks to the south (refer to online Supplementary material, Fig. S1; Taucher et al. 2013). Notably, the Medicine Bow Mountains, unlike the Sierra Madre Mountains, contain a thick band of metasedimentary rocks that form the Snowy Range (Taucher et al. 2013).

The UNPR Basin, which consists of the North Platte River and its tributaries upstream of Seminoe Reservoir, Wyoming, is biologically productive, sustaining an estimated 2500 brown and rainbow trout per kilometre in the main stem of the UNPR (McDowell 1983). The UNPR basin has supported robust populations of wild brown and rainbow trout since 1884 (McDowell 1983). Our study incorporated water and fish samples from 23 perennial tributaries and the North Platte River in the upper 47% of the 7665 km<sup>2</sup> basin (Figs. 1 and 2).

### Water collection

To assess the spatial variation of  $^{87}\text{Sr}/^{86}\text{Sr}$  and establish baseline  $^{87}\text{Sr}/^{86}\text{Sr}$  signatures for the stream reaches relevant to fish movement, we collected water samples at 57 locations across 21 tributaries and the main stem of the North Platte River between June and October 2015 (Fig. 1). Each of the 21 tributaries had one to five collection locations, and the North Platte River had nine collection locations. We stratified collection locations longitudinally along tributaries to encompass variation in underlying geology and stream network dynamics. At one location in French Creek and one location in Big Creek, we collected water samples three

times throughout the year (June, August, and October) to estimate seasonal variation in  $^{87}\text{Sr}/^{86}\text{Sr}$ . We collected water samples in the thalweg of each stream at an intermediate depth in the water column.

We collected water samples in clean, acid-washed 250 mL Nalgene high-density polyethylene bottles and stored samples in a Ziplock bag. Within 48 h of collection, we filtered samples through a 0.45 µm sterile syringe filter into a clean, acid-washed, 125 mL Nalgene high-density polyethylene bottle using a 60 mL syringe. Once filtered, we placed samples in a Ziplock bag, transported them to the University of Wyoming, and refrigerated until analysis. To evaluate error in field collection and filtration methods, we collected samples at six sites in triplicate. At each triplicate sampling location, we also took a blank sample using high-purity deionized water (DI; Evoqua, 12 Mohm). Filtration methods were similar to those outlined in Shiller (2003).

### Fish collection and otolith preparation

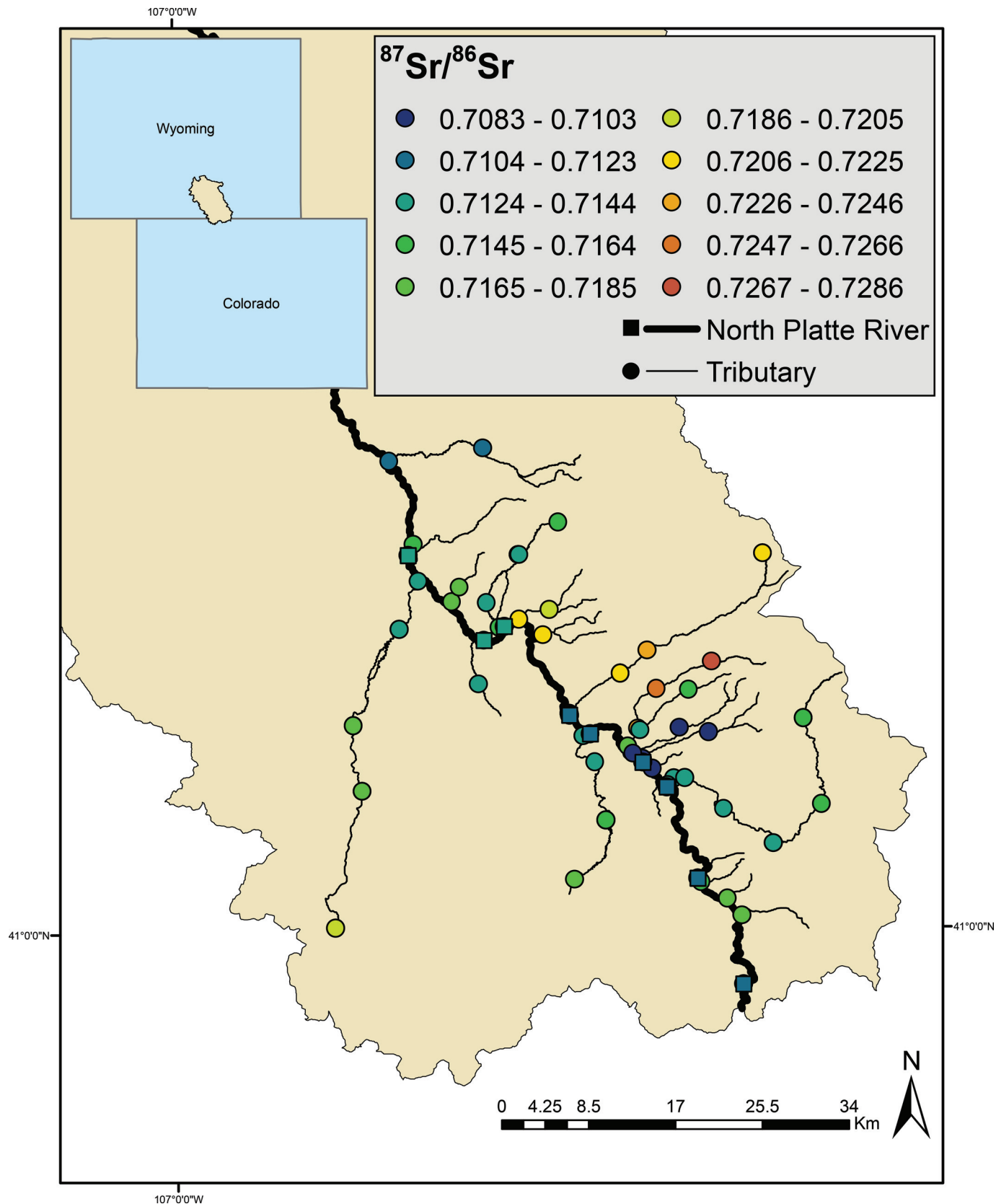
To evaluate the proportion of each population that are migrants and identify the migration diversity of brown and rainbow trout migrants, we developed a fish capture sampling scheme that allowed us to identify migration variants from all cohorts of fish captured throughout the study area. We collected 2 fish·km<sup>-1</sup> (one brown trout and one rainbow trout) from the main stem of the North Platte River between the Colorado–Wyoming border, river km 11.5, to just downstream of the town of Saratoga at river km 100.5, with several exceptions. We captured two rainbow trout at three sites and two brown trout at four sites. We captured no fish at one site and no rainbow trout at an additional three sites. In total we collected 89 brown trout and 87 rainbow trout. Owing to logistical constraints of the study area, we used two sampling approaches to collect fish: hook-and-line and raft electrofishing. Between river km 11.5 and 31.5, we used hook-and-line sampling and collected the first fish of each species caught per kilometre. Upon capture, we euthanized individuals with MS-222, recorded their total length (TL), and extracted their sagittal otoliths. Between river km 31.5 and 100.5, we used raft electrofishing. For this portion of the river, we used a stratified random sampling scheme to capture fish. We assigned length bins to each kilometre section. Per 6 km, we randomly assigned one of six fish length bins (<100, 100–200, 200–300, 300–400, 400–500, >500 mm) to each kilometre. Using a stratified random sampling scheme eliminated the size sampling bias presented by raft electrofishing, ensuring we would capture fish from all cohorts present. During sampling, we captured and placed all fish in a live well. If we could not capture fish in the desired length bin, we euthanized the fish that were closest to the desired length. We placed euthanized fish on ice, transported them to the University of Wyoming, and froze them until processing. Once in the lab, we thawed the fish, measured their TL, and extracted their sagittal otoliths.

To explore spawning site fidelity expressed by rainbow trout, we collected, using a backpack electrofisher, two to five ripe (i.e., eggs or milt released from body when palpated) or spent (i.e., sagging abdomen in females) rainbow trout in North Cottonwood Creek, Cottonwood Creek, Savage Run Creek, Cedar Creek, Mulen Creek, French Creek, and Big Creek for a total of 28 fish. Upon capture, we euthanized each fish using MS-222, measured their length, and extracted their sagittal otoliths. While we would have liked to assess spawning site fidelity of brown trout, we were unable to capture ripe or spent brown trout.

To quantify our ability to assign fish of an unknown origin to a sampling location, we collected juvenile fish in tributaries prior to their potential outmigration to the main stem of the North Platte River. We used a backpack electrofisher to capture three to seven juvenile (30–99 mm long) brown, rainbow, or brook trout (*Salvelinus*

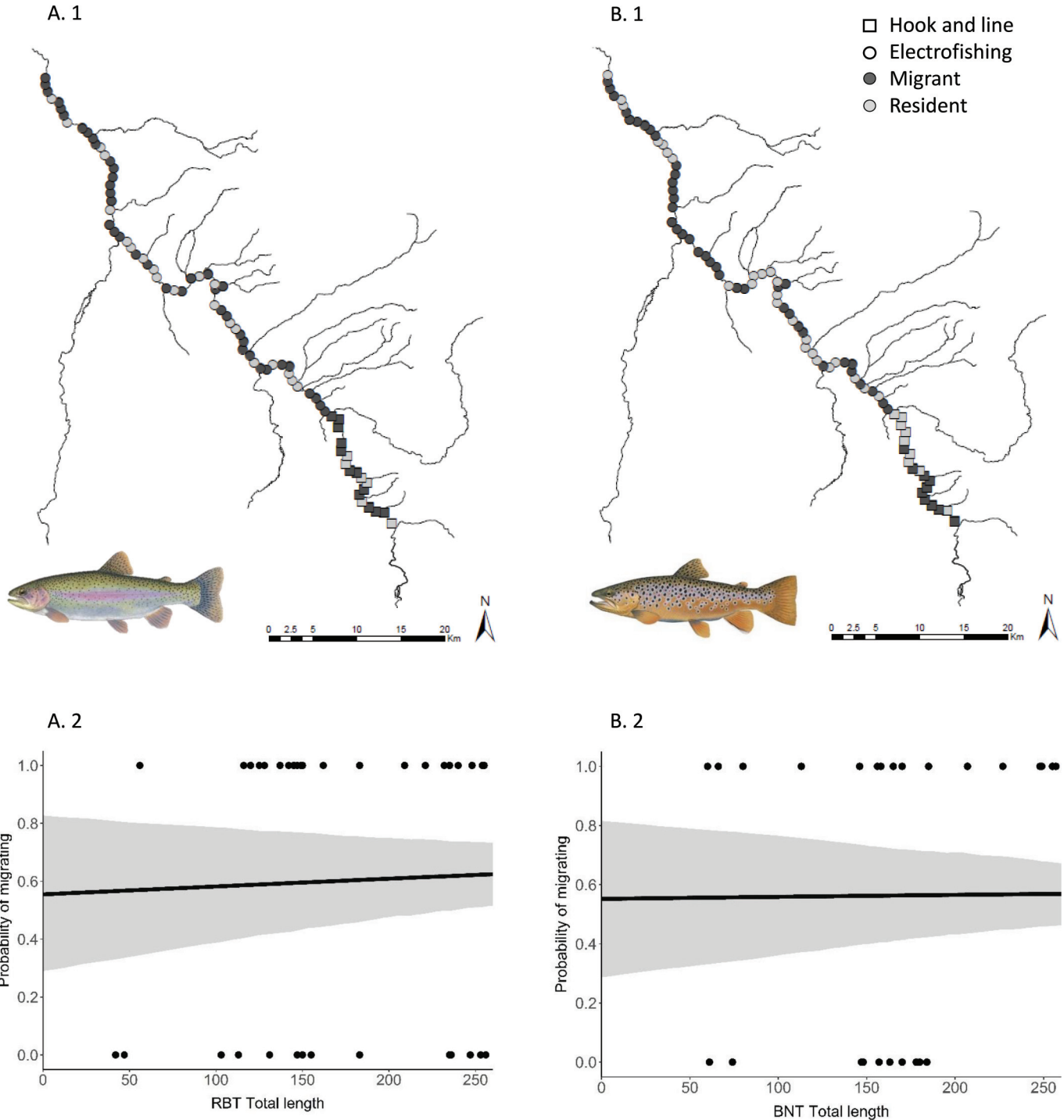
<sup>1</sup>Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2018-0087>.

**Fig. 1.** Large spatial overlap was observed in surface water  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios measured at 57 locations in 21 tributaries (circles) and the main stem (squares) of the Upper North Platte River in the Upper North Platte River Basin, Wyoming, USA. Samples were collected June–October 2015. This map was created using ArcGIS software by Esri. [Colour online.]



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**Fig. 2.** Both migrant and resident rainbow trout (A. 1) and brown trout (B. 1) were captured throughout the main stem of the Upper North Platte River. Rainbow trout (A. 2) and brown trout (B. 2) probability of being a migrant was not related to fish size. Black dots represent observed data. Black lines show predicted values, and shaded bands reflect nonparametric, bootstrapped 95% confidence intervals for predicted values from a logistic regression. Fish were collected from the Upper North Platte River Basin in Wyoming, USA, July–August 2015. Fish images courtesy of the Kentucky Department of Fish and Wildlife Resources, Rick Hill artist.



*fontinalis*) at one to two locations on six tributaries for a total of nine sampling locations. We targeted juvenile salmonids because, of all fish we were able to consistently find in the basin (*Cottus* spp. and *Rhinichthys* spp. were rarely encountered), they were the most likely to exhibit limited movement. After collection, we placed juvenile trout in a 95% ethanol solution and transported them back to the University of Wyoming where we measured their total

lengths and extracted their sagittal otoliths. All fish were treated humanely, and the methods were approved by the University of Wyoming Institutional Animal Care and Use Committee protocol No. 20150507AW00160-01.

After extraction, we prepared otoliths for aging and laser ablation following methods outlined in [Stevenson and Campana \(1992\)](#) and [Wolff et al. \(2012\)](#). We sonicated all otoliths for 3 min in

Milli-Q water. We mounted juvenile otoliths (fish TL  $\leq$  160 mm) with Crystalbond 509, sculus side down, on a glass cover slip. We then hand-polished otoliths using 30, 9, and 2  $\mu\text{m}$  wet-dry polishing paper in sequence, until the core and daily growth rings were detected. We then affixed otoliths to a petrographic slide using superglue. We embedded adult otoliths (fish TL  $>$  160 mm) in epoxy resin and cut the otoliths transversely, using an Isomet low-speed saw with two diamond wafering blades and a 1 mm spacer. We hand-polished adult otolith sections to a thickness of 0.65 mm using 30, 9, and 2  $\mu\text{m}$  wet-dry polishing paper. At this thickness, the core and all yearly rings were exposed. Once polished, we mounted sections to a petrographic slide using superglue. Prior to  $^{87}\text{Sr}/^{86}\text{Sr}$  analysis, we transferred all petrographic slides to a clean room where we rinsed and sonicated otoliths in DI water for 3 min and let dry under a class 100 laminar flow hood.

### $^{87}\text{Sr}/^{86}\text{Sr}$ analysis

We sent water samples to the University of Utah, Department of Geology and Geophysics, ICPMS laboratory for  $^{87}\text{Sr}/^{86}\text{Sr}$  analysis where they were analyzed using methods outlined in Brennan et al. (2015b). Briefly, water samples were analyzed for  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios using multicollector inductively coupled plasma mass spectrometry (MC-ICPMS; Thermo Scientific, High Resolution NEPTUNE, Bremen, Germany) and the University of Utah's introduction system to purify Sr for  $^{87}\text{Sr}/^{86}\text{Sr}$  analysis of aqueous solutions. Using these methods, Brennan et al. (2015b) found the long-term replicability of the NIST SRM987 ( $^{87}\text{Sr}/^{86}\text{Sr} = 0.71030 \pm 0.00026$  95% confidence interval; [www.nist.gov](http://www.nist.gov)) to be  $^{87}\text{Sr}/^{86}\text{Sr} = 0.71030 \pm 0.00004$  (2 SD).

During water sample analysis reported here, the weighted daily mean  $\pm$  2 SD of the NIST SRM987 ratio was  $0.71029 \pm 0.00003$  ( $n = 5$ ). Field triplicate analysis of collected water samples revealed low variation (2 SD =  $\pm 0.00006$ ) between samples from the same sampling location ( $n = 6$ ).

We analyzed otolith samples for  $^{87}\text{Sr}/^{86}\text{Sr}$  at Woods Hole Oceanographic Institution Plasma Mass Spectrometry Facility, Woods Hole, Massachusetts, using a Thermo Finnigan Neptune MC-ICP-MS coupled to a laser ablation system (New Wave Research UP 193 nm excimer laser). We configured the laser to run at 90% intensity with a 10 Hz pulse rate, 50  $\mu\text{m}$  beam size, and a scanning speed of 2  $\mu\text{m}\cdot\text{s}^{-1}$ . Once ablated, otolith material was carried from the laser cell to the MC-ICP-MS where a suite of isotopes ( $^{88}\text{Sr}$ ,  $^{87}\text{Sr}$ ,  $^{86}\text{Sr}$ ,  $^{85}\text{Rb}$ ,  $^{83}\text{Kr}$ , and  $^{82}\text{Kr}$ ) were measured with an integration time of 2.097 s. These settings are similar to those used in Wolff et al. (2012) and Brennan et al. (2015b). We ran single laser ablation transects from the core to the dorsal edge of the 176 adult otoliths and from the core to the dorsal or ventral edge of the 39 juvenile otoliths. This method allowed us to capture a strontium isotope ratio profile across each individual's entire life. Prior to each ablation transect, we measured background intensities of each isotope for 120 cycles and used the mean as a blank correction during the run. We ran the US Geological Survey Microanalytical Carbonate Standard, MACS-3 ( $^{87}\text{Sr}/^{86}\text{Sr} = 0.70759 \pm 0.00005$  1 SD; [crustal.usgs.gov](http://crustal.usgs.gov)) every 15–20 samples to monitor machine drift and precision ( $n = 36$ ). Mean ( $\pm$  1 SD)  $^{87}\text{Sr}/^{86}\text{Sr}$  of MACS-3 was  $0.70771 \pm 0.00006$ .

For comparison of water and otolith samples between labs, we normalized all samples to the standards using the following equation:

$$^{87}\text{Sr}/^{86}\text{Sr} \text{ normalized} = \left( \frac{S_p}{S_m} \right) \times ^{87}\text{Sr}/^{86}\text{Sr}$$

where  $S_p$  is the published standard value, and  $S_m$  is the average measured standard value. Otolith and water  $^{87}\text{Sr}/^{86}\text{Sr}$  samples were corrected for mass bias using an exponential law and for isobaric interferences (Brennan et al. 2015b). Normalized otolith

and water sample data can be found in the online Supplementary material, data sets S1–S4<sup>1</sup>.

### Otolith aging

After laser ablation, we photographed otoliths using an Olympus SZX16 research stereomicroscope system and attached Olympus Q-Color5 digital imaging system. Two experienced otolith agers then independently aged otoliths under the stereomicroscope. During aging the first feeding check and each annuli was marked, along the laser ablation transect, on each otolith picture. Where recorded ages, location of the first feeding check, or location of annuli differed between the two reads, the two otolith agers discussed the age of the otolith and the location of the first feeding check or annuli. If agers could not agree on otolith age, first feeding check, or annuli location, the otolith was excluded from analyses. Of the 176 UNPR otoliths, three could not be aged, and the location of the first feeding check or annuli for an additional four could not be agreed upon. For successfully aged otoliths, we plotted the location of the first feeding check and annuli on the strontium isotope ratio profiles. For all further analyses, we considered isotopic data recorded from laser ablation transects running from the first feeding check to the outer edge of the otolith. We excluded  $^{87}\text{Sr}/^{86}\text{Sr}$  signatures deposited prior to the first feeding check because of the bias maternal influence can have on prefeeding isotopic signatures (Miller and Kent 2009). Hegg et al. (2019) found that initial changes from maternal  $^{87}\text{Sr}/^{86}\text{Sr}$  signatures to ambient water  $^{87}\text{Sr}/^{86}\text{Sr}$  appeared to correspond to the hatching of larval Chinook salmon (*Oncorhynchus tshawytscha*) and continued until equilibrium with ambient water was reached near the onset of exogenous feeding.

### Rainbow and brown trout migrant identification

We conducted a pruned exact linear time changepoint analysis on normalized, unfiltered  $^{87}\text{Sr}/^{86}\text{Sr}$  profiles and applied a two-tiered decision-making process to assess whether an individual fish was a migrant. We first used the {changepoint} package in R to identify changepoints (i.e., the first observation of a new segment) based, simultaneously, on changes in the mean and variance of recorded  $^{87}\text{Sr}/^{86}\text{Sr}$  (Killick et al. 2012). We used the default penalty algorithm, MBIC (modified Bayes information criterion), in the {changepoint} package. We then calculated the mean  $^{87}\text{Sr}/^{86}\text{Sr}$  of each segment identified by the changepoint analysis and applied two sets of criteria (i.e., tier one and tier two) to establish migrant status (i.e., migrant or nonmigrant) of each fish. Tier one fish were classified as a migrant if the individual's natal otolith segment (segment located between the first feeding check and the first changepoint) mean value fell more than 0.00064 outside the range of the UNPR's  $^{87}\text{Sr}/^{86}\text{Sr}$  signature (0.71183–0.71331) and as a nonmigrant if the individual's natal otolith segment mean value fell within  $\pm 0.00064$  the range of the UNPR's  $^{87}\text{Sr}/^{86}\text{Sr}$  signatures and the individual's full strontium profile did not contain a changepoint. For those fish whose migration status was not identified using tier one criteria, we applied tier two criteria to establish migration status. Tier two fish were classified as a migrant if their natal otolith segment mean value differed from the segment mean value immediately following their natal otolith segment by more than 0.00064 and as a nonmigrant if the difference was less than 0.00064. We considered isotopic shifts above 0.00064 biologically meaningful, indicating fish movement events and not the result of seasonal  $^{87}\text{Sr}/^{86}\text{Sr}$  variations, because 0.00064 was our observed seasonal variation in both French and Big creeks (Data set S1<sup>1</sup>).

We believe the fish classified as migrants based on tier two criteria are not fish that made large-scale movements within the UNPR because (i) fish who are born in the UNPR and move throughout the UNPR contain gradual changes ( $< 0.00064$ ) between segment mean values because UNPR's  $^{87}\text{Sr}/^{86}\text{Sr}$  signature gradually changes from upstream to downstream (Ciepiela and

Walters 2019) and (ii) fish who were born in tributaries with overlapping  $^{87}\text{Sr}/^{86}\text{Sr}$  signatures to the UNPR contain a difference of greater than 0.00064 between natal and adjacent segment mean values because for each tributary ( $n = 6$ ) whose strontium signatures overlaps with the UNPR's signature, the difference between the tributary's  $^{87}\text{Sr}/^{86}\text{Sr}$  signatures and the UNPR's  $^{87}\text{Sr}/^{86}\text{Sr}$  signature, near the tributary confluence, is greater than 0.00064 (Data set S1; Ciepiela and Walters 2019).

Once we established individual migration status, we used logistic regression to examine the relationship between migration status and fish size because the size distribution of captured fish varied between the two sampling methods (hook-and-line and raft electrofishing).

### Tributary use of brown and rainbow trout migrants

We used two approaches to investigate tributary use of UNPR migrants. First, we applied an assignment model to identify probable natal streams of origin for each fish. We then developed a second approach to visualize and compare the distribution of natal otolith segment  $^{87}\text{Sr}/^{86}\text{Sr}$  between species. Observing differences in the distribution of  $^{87}\text{Sr}/^{86}\text{Sr}$  is assumed to correspond to use of isotopically differing tributaries. We developed the second approach for comparing  $^{87}\text{Sr}/^{86}\text{Sr}$ , and thus habitat use, within and between populations because we were unable to draw meaningful conclusions about fish origin and thus diversity of fish migration pathways using the assignment methods (see Results section).

### Assignment model

We used a modified likelihood-based assignment approach to identify probable natal tributaries of brown and rainbow trout migrants and spawning rainbow trout. We first built a normally distributed probability density function that incorporated both within-site and analytical variance for each otolith. We set the mean of each probability density function equal to the mean of the  $^{87}\text{Sr}/^{86}\text{Sr}$  measured in each otolith's natal segment. We used the mean 95% prediction interval (0.00196) from a regression of known origin otolith  $^{87}\text{Sr}/^{86}\text{Sr}$  signatures to matching water  $^{87}\text{Sr}/^{86}\text{Sr}$  signatures (slope  $\pm$  SE =  $1.034 \pm 0.0165$ , intercept  $\pm$  SE =  $-0.024 \pm 0.01184$ ,  $n = 39$ ) to represent standard deviation (SD) because the difference between natal segment and matching water  $^{87}\text{Sr}/^{86}\text{Sr}$  reflects both within-site and analytical error (Brennan and Schindler 2017). We set SD equal to one-half the mean 95% prediction interval. We then assessed whether each measured surface water strontium isotope ratio fell within the strontium isotope ratio range associated with the 95% quantile-based confidence region of each otolith's probability density function. We considered all source locations that fell within the strontium isotope ratio range associated with the 95% quantile-based confidence region as reasonable candidate source locations and those that fell outside of the 95% quantile-based confidence region as unlikely candidate source locations. The accuracy of our assignment approach was tested through the collection and analysis of the juvenile salmonids collected from known tributary origins at locations where water samples were also collected.

Our assignment method allowed us to probabilistically infer fish origin while incorporating analytical and within-site error, which is an improvement over cluster-based assignment methods and similar to other likelihood-based assignment methods (see Wunder and Norris 2008; Wunder 2010; Brennan and Schindler 2017). Cluster-based assignment methods, like classification trees (Hebert and Wassenaar 2005), assign origin based on a series of hierarchical discrimination-based decision rules. These methods do not incorporate most error and are unable to assign degrees of certainty to each group (Hebert and Wassenaar 2005; see Wunder and Norris 2008). Our assignment method is similar to other likelihood-based assignment methods. In both cases, origin is inferred from a probability density function (Barnett-Johnson et al.

2008; Wunder 2012). This allows for the incorporation of some sources of error and provides probability of assignment (see Wunder and Norris 2008). The primary difference between our model and other likelihood-based assignment models used for inferring origin is the data underlying the probability density function. We inferred fish origin using the otolith natal segment strontium isotope ratio mean to parameterize the density functions. Other studies infer natal origin using the landscape strontium isotope ratio data to parametrize the probability density functions (Barnett-Johnson et al. 2008; Wunder 2012; Brennan et al. 2015a). Establishing a probability density function for each otolith, opposed to one for each water location, allowed us to assess the probability an otolith's natal segment was synthesized in each water source independently of all other water sources. This was advantageous because we did not have to carve up space into nominal isotope groups, meaning we were able to identify water sources with overlapping signatures as equally probable. Ultimately, because we observed high overlap of surface water strontium isotope rates, with many sites falling throughout the 95% quantile-based confidence region, we chose to take a conservative approach to inferring origin and assumed all locations within the prediction interval were possible; however, we could have easily selected a probability threshold and only considered sites as probable above a given threshold.

### Otolith $^{87}\text{Sr}/^{86}\text{Sr}$ distribution

To explore and compare the range of strontium isotope ratio signatures measured in the natal otolith segments of brown and rainbow trout migrants, which is representative of the range of tributary habitat use, we used the normalized strontium isotope ratio values measured in each individual's natal otolith segment to calculate the maximum likelihood best-fit parameters of the normal distribution (mean and SD). We plotted the natal otolith segment mean along a strontium isotope ratio gradient that encompassed the surface water  $^{87}\text{Sr}/^{86}\text{Sr}$  measured in tributaries throughout the UNPR Basin. We then used a sliding window analysis to count the number of fish (means) along the strontium isotope ratio gradient to establish a distribution of strontium isotope ratio use. For the sliding window analysis, we used a bin size of 0.0004 with values along the strontium isotope ratio gradient sequenced from 0.708 to 0.730 by 0.0001. By plotting the mean of each natal otolith segment and conducting a sliding window analysis on the mean, we could (i) quantify the range of strontium isotope ratio values used by each species and (ii) observe the distribution of use along the strontium isotope ratio gradient for each species.

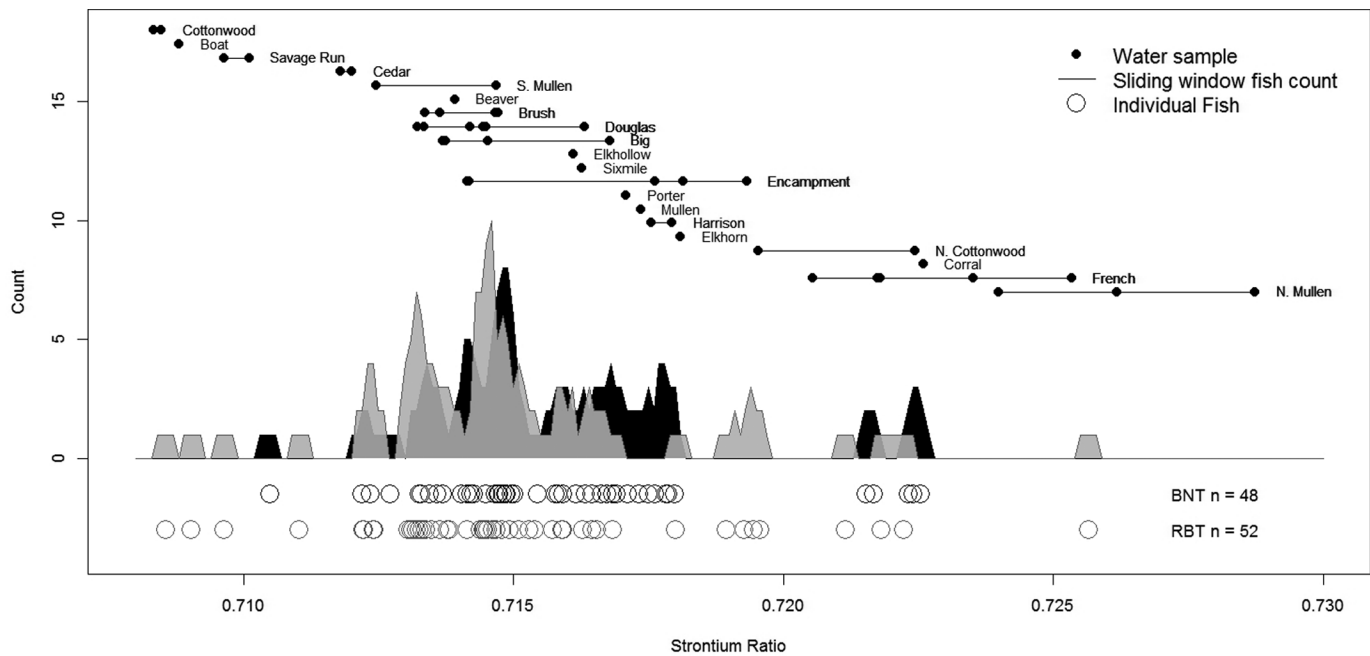
### Age at movement

We also assessed the length of time individuals spent in the tributary for each population. To determine length of time in the tributary, we recorded the age at which the UNPR  $^{87}\text{Sr}/^{86}\text{Sr}$  signature (0.71183–0.71331) was first detected and considered this the age at immigration into the UNPR.

### Spawning rainbow trout

To assess rainbow trout straying rates, we compared the capture tributary of the 27 spawning rainbow trout with the list of source candidate tributaries generated for each fish by the assignment model. We classified individuals as strayers, if their capture tributary was not one of the candidate source tributaries, and as a returner, if their capture tributary was one of the candidate source tributaries. We also determined age at movement from natal site for all spawners by combining the pruned exact linear time changepoint analysis with the aging data as described above for the mainstem migrants. We used a Welch two-sample  $t$  test to assess the difference in age at movement between strayers and returners.

**Fig. 3.** Rainbow trout (grey) and brown trout (black) strontium isotope ratio distribution of use, synonymous to habitat use, was revealed through a sliding window analysis. Individual rainbow trout (grey circles) and brown trout (black circles) mean natal otolith segment strontium ratios are plotted below the distributions, along the strontium gradient to quantify the range of strontium values used by each population. The surface water strontium ratios measured in tributaries of the Upper North Platte River are plotted above the natal use distributions for reference. Fish were collected from the Upper North Platte River Basin in Wyoming, USA, July–August 2015.



We conducted all analyses using R version 3.3.0 (R Core Team 2016). We conducted the changepoint analysis using the {changepoint} package (Killick and Eckley 2014, 2016).

## Results

### Surface water $^{87}\text{Sr}/^{86}\text{Sr}$

Despite observing a large range in surface water strontium isotope ratio signatures across the UNPR Basin, strontium isotope ratio signatures in tributaries were neither individually nor spatially distinct (Fig. 1; Data set S1<sup>1</sup>). Surface water  $^{87}\text{Sr}/^{86}\text{Sr}$  ranged from 0.70825 to 0.72865 (Figs. 1 and 3). Additionally, we recorded variable longitudinal variation within tributaries. Of the tributaries where more than one sampling location occurred, the Encampment River had the largest longitudinal  $^{87}\text{Sr}/^{86}\text{Sr}$  variation, which ranged from 0.71415 to 0.71933, while Cottonwood Creek had the smallest longitudinal  $^{87}\text{Sr}/^{86}\text{Sr}$  variation, ranging from 0.70834 to 0.70848. We recorded seasonal variation in both French Creek and Big Creek. French Creek surface water  $^{87}\text{Sr}/^{86}\text{Sr}$  ranged from 0.72167 to 0.72195 ( $n = 3$ ;  $\text{SD} = 0.00064$ ). Big Creek surface water  $^{87}\text{Sr}/^{86}\text{Sr}$  ranged from 0.71389 to 0.71517 ( $n = 2$ ;  $\text{SD} = 0.00064$ ). The overlapping tributary signatures coupled with the large longitudinal variation made inferring specific tributary natal origin impossible.

### Tributary migrants

We were able to use data from 85 brown trout and 84 rainbow trout collected from 89 km of the main stem of the UNPR. Rainbow trout ranged in TL from 42 to 473 mm and in age from 0 to 13. Brown trout ranged in TL from 60 to 602 mm and in age from 0 to 11. We found that 63% of rainbow trout and 57% of brown trout were migrants (Fig. 2; Data set S2<sup>1</sup>).

We captured a smaller size distribution of fish using hook-and-line sampling compared with raft electrofishing. Rainbow trout captured using hook-and-line sampling ( $n = 19$ ) ranged in TL from 149 to 378 mm and in age from 1 to 6 years. Rainbow trout captured using electrofishing ( $n = 65$ ) ranged in TL from 42 to 473 mm

and in age from 0 to 13 years. Brown trout captured using hook-and-line sampling ( $n = 19$ ) ranged in TL from 295 to 451 mm and in age from 3 to 7 years. Brown trout captured using electrofishing ( $n = 66$ ) ranged in TL from 60 to 602 mm and in age from 0 to 11 years. We found no statistically significant relationship between the size of the individual and their probability of being a migrant (Fig. 2).

### Tributary use of UNPR fish

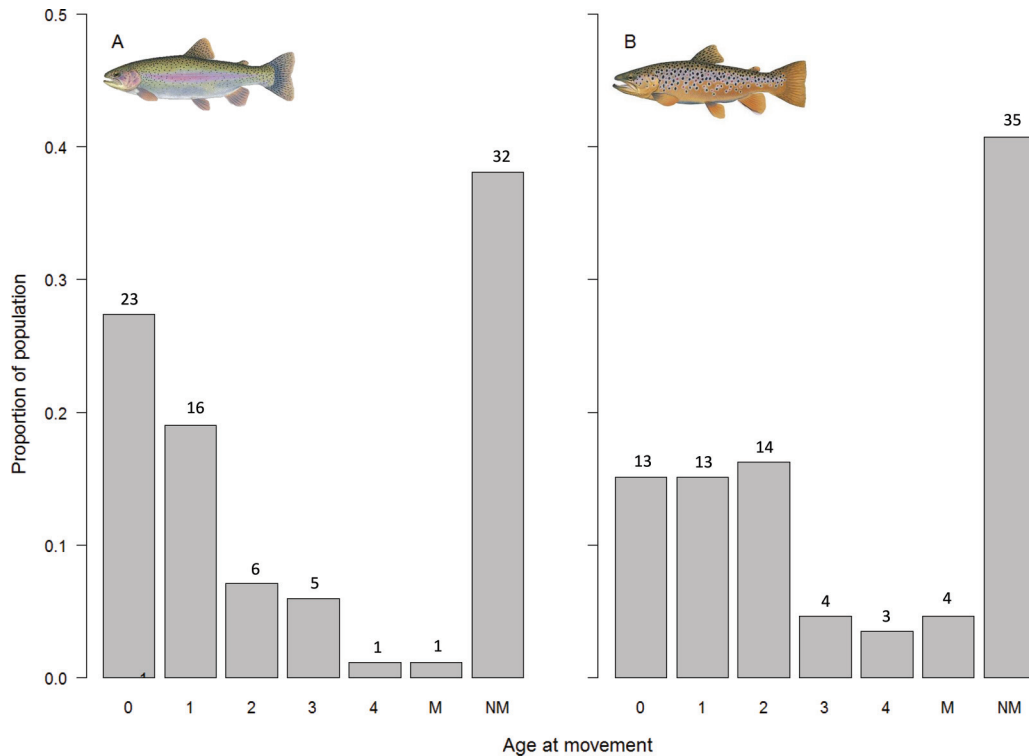
#### Assignment model

We were unable to identify a single stream of origin for the majority of fish, but we are confident that each individual's true stream of origin made the fish's candidate source list. We assigned juvenile fish, of known origin, to one to seven candidate streams. For these fish, their true stream of origin made the candidate stream of origin list 100% of the time. We assigned fish from the main stem of the UNPR and the spawning rainbow trout to one to eight candidate streams of origin (see Tables S1–S2<sup>1</sup> for a complete list of candidate streams of origin for each mainstem brown and rainbow trout). Based on a compilation of the candidate streams of origin generated for each fish, we are confident no brown trout captured in the main stem of the UNPR originated from North Fork of Mullen Creek, Cottonwood Creek, or Boat Creek. We could not eliminate any tributaries as a stream of origin for rainbow trout.

#### Otolith $^{87}\text{Sr}/^{86}\text{Sr}$ distribution

Both species used a large range of the available tributary habitat. For both species, there was a continuous and heavy distribution of use between 0.713 and 0.718. This area likely represents the core tributary habitat. Interestingly, the core tributary habitat only included 67% of the rainbow trout migrants, while it included 81% of the brown trout migrants. Rainbow trout natal otolith segments were distributed along the strontium isotope ratio gradient from 0.70856 to 0.72566, whereas natal otolith segments of brown trout were distributed along the strontium isotope ratio

**Fig. 4.** Rainbow trout (A) and brown trout (B) age at migration ranged from 0 to 4. Rainbow trout age at migration was skewed right, while brown trout age at migration was uniformly distributed between ages 0 and 3. M indicates the proportion of the population where a natal migration event was detected but the otolith was not successfully aged. No migration (NM) was detected in 37% and 43% of the rainbow and brown trout populations, respectively. The number of fish recorded in each bin are written above each bin. Fish were collected from the Upper North Platte River Basin in Wyoming, USA, July–August 2015. Fish images courtesy of the Kentucky Department of Fish and Wildlife Resources, Rick Hill artist.



gradient from 0.71049 to 0.72254 (Fig. 3). Overall rainbow trout migrants used a larger range of the available tributary habitat than brown trout.

#### Age at movement

For brown and rainbow trout classified as migrants, the range in age at movement was equal (0–4); however, the distribution differed between the two species (Fig. 4). The distribution of age at movement for rainbow trout was skewed right, towards age 0, with 75% of the migrants moving into the UNPR by age 2. The distribution of age at movement for brown trout was more uniformly distributed with only 51% of the migrants moving into the UNPR by age 2. We were unable to determine the age of movement into the UNPR for one rainbow trout and four brown trout.

#### Rainbow trout straying

Most rainbow trout strayed from their natal group of candidate streams; however, tributary-specific straying rates were variable. In total, 15 of 26 (56%) spawning rainbow trout strayed from their natal group of candidate streams, with 8 of 11 males (73%) and 7 of 15 females (47%) straying from their natal group of candidate streams to spawn. Straying rates between sites ranged from 100% at Cottonwood Creek (a small tributary) to 0% at French Creek and Big Creek (the largest tributaries; Fig. 5; Data set S4<sup>1</sup>). Mean age at movement for fish classified as strayers was 0.5 ( $n = 14$ ), which was significantly lower (Welch two-sample  $t$  test;  $p$  value = .026) than the mean age of movement for returners (1.36,  $n = 11$ ). Because we were unable to identify a single stream of origin, these straying rates are likely conservative.

## Discussion

### Migration diversity

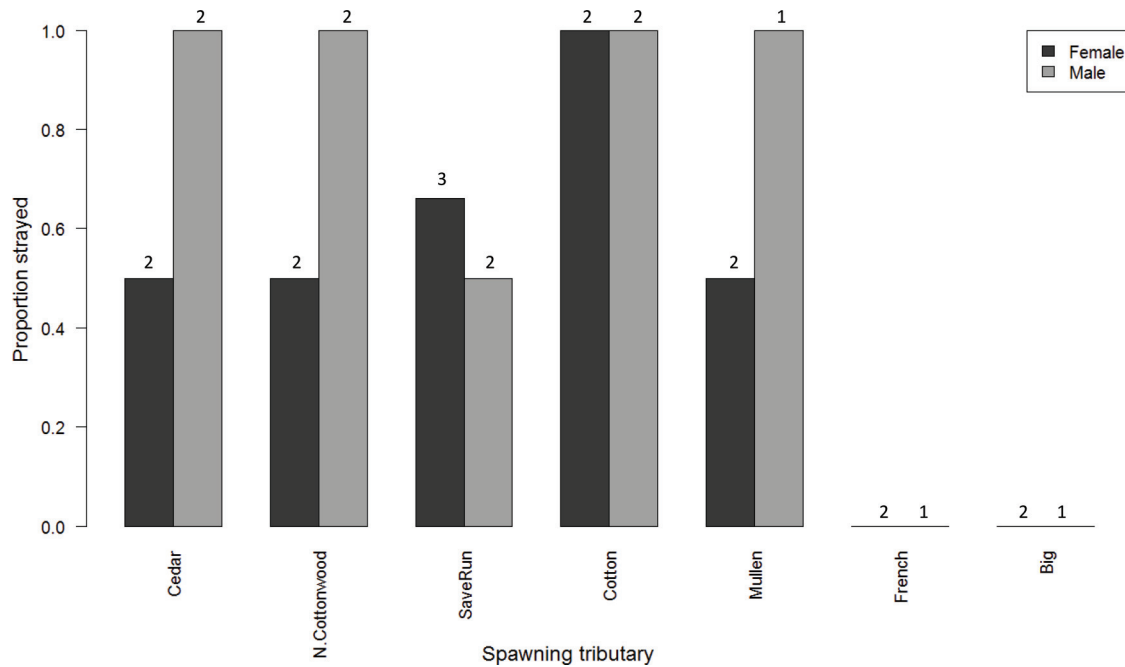
A wide range of life-history strategies exists within and between the UNPR rainbow and brown trout populations. There were two distinct primary juvenile migration strategies: to migrate from tributaries into the UNPR after hatching or to remain a resident of their natal river, the UNPR. 63% of rainbow trout and 57% of brown trout migrated between natal and resident locations. These estimates are potentially conservative because the degree to which downstream movement into the UNPR occurred prior to the establishment of a natal tributary signature is unknown.

Muhlfeld et al. (2012) used similar otolith microchemistry techniques to reconstruct the environmental history of westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) in the Flathead River drainage and found 44% of the population had migrated from a natal stream into a resident location. Our migration results indicate juvenile fish are capable of extensive movements, which supports the findings of Muhlfeld et al. (2012).

A closer examination of the specific migration strategies expressed by brown and rainbow trout revealed that the two species may use tributaries to differing extents. As a population, brown trout uniformly diversified their age at movement between 0 and 3 but use a smaller range of the strontium isotope ratio gradient and therefore spawning habitat than rainbow trout. Rainbow trout display a smaller range in age at movement, with most rainbow trout having migrated out of their natal stream by age 2. Rainbow trout use a wider range of the strontium isotope ratio gradient, indicating they can use more tributaries and spawning habitat within tributaries than brown trout can. Both species are spreading risk and production across tributaries and cohorts, but



**Fig. 5.** Both male and female spawning rainbow trout contributed to the total proportion of captured spawning rainbow trout that had strayed from their natal stream of origin to spawn in the small tributaries (20–68 km<sup>2</sup>). In French Creek and Big Creek, the two largest tributaries (160 and 514 km<sup>2</sup>, respectively), we did not identify any strays. The sample size for each category is written above each bar. Spawning rainbow trout were collected from the Upper North Platte River Basin in Wyoming, USA, May 2016.



our results suggest brown trout rely more on temporal distribution of risk among offspring, whereas rainbow trout rely more on spatial distribution of risk among offspring to distribute risk. Our conclusions are limited by sample size of migrants, but there is no suggestion that propensity to migrate varied spatially or temporally (Fig. 2), so our expectation is that a larger sample size would only strengthen the patterns seen.

The migration strategies expressed by brown and rainbow trout fall along the spectrum of migration strategies observed within and between populations of Pacific salmon. For example, on one end of the spectrum, pink salmon (*Oncorhynchus gorbuscha*) show little variation in age at smolting and age at maturity, leaving little space to distribute environmental risk between cohorts. Instead pink salmon rely on productivity across the landscape to spatially distribute environmental risk (Waples et al. 2009). On the other end of the spectrum, Chinook salmon distribute risk across cohorts by expressing larger variation in age at smolting and age at maturity (Waples et al. 2009). Rainbow and brown trout appear to use similar strategies to spread environmental risk as Pacific salmon.

#### Mechanisms that promote migration diversity

We hypothesize the differences in specific migration strategies used by rainbow and brown trout are due to the environmental conditions during each species spawning season. Brown trout spawn in autumn when discharge is near base flow, while rainbow trout spawn in the spring during spring runoff. In autumn, smaller tributaries in the UNPR Basin, like Cottonwood Creek, Sixmile Creek, and Savage Run, may not hold adequate water for brown trout spawning. Additionally, overwintering conditions (i.e., freezing temperatures and shallow water) in tributaries may not be suitable for brown trout eggs. Freezing temperatures and shallow water are not limitations for rainbow trout eggs because they spawn in the spring. However, because rainbow trout spawn in the spring, their offspring face ever diminishing flows throughout the rearing season, potentially explaining why we observed

younger age at movement for rainbow trout than we did for brown trout.

#### Rainbow trout straying

Of the captured spawning rainbow trout, 53% had strayed from their natal stream to spawn. Across species and populations, salmonids show large variation in straying rates, with the balance of homing and straying contributing to the overall resiliency and genetic diversity of individual populations (Walter et al. 2009; Keefer and Caudill 2014). Straying from natal streams promotes genetic mixing and allows for the exploration and colonization or recolonization of new or previously damaged habitat, but often at a fitness cost. By contrast, homing allows species to increase their overall fitness by adapting to specific environmental conditions (Lin et al. 2008).

Strayers left their natal tributary, on average, 0.86 years earlier in life than fish that were potential returners. While salmonid homing is guided by olfactory recognition and imprinting (Dittman and Quinn 1996; Ueda 2012), the mechanisms that lead to straying are not as well understood (Keefer and Caudill 2014). Our finding supports the idea that juvenile dispersal is associated with straying. Hamann and Kennedy (2012) explored the factors underlying individual straying behavior and found, similar to our findings, that high rates of juvenile exploration and natal dispersal were associated with higher straying rates. It is possible that early juvenile movement and dispersal may inhibit an individual's ability to properly imprint and thus ability to return to their stream of origin.

We observed high straying rates (60%–100%) in the smaller tributaries (20–68 km<sup>2</sup>). In French Creek and Big Creek, our largest tributaries (160 and 514 km<sup>2</sup>, respectively), we did not capture any strays. We suggest juvenile dispersal and straying may be linked to tributary environmental conditions. Smaller tributaries, like Cottonwood Creek, likely do not provide adequate rearing habitat, motivating juveniles to explore other habitat perhaps prior to imprinting, while the larger tributaries, like French and Big

creeks, provide adequate spawning and rearing habitat, enabling fish to rear longer and imprint. Overall, we hypothesize these differences in spawning habitat types promote the variation in observed straying behaviors, with the larger tributaries promoting fish that home, whereas smaller tributaries promote strayers.

### Otolith microchemistry limitations

Using otolith microchemistry allowed us to describe the migratory behaviors of rainbow and brown trout individuals and thus the diversity of movement strategies expressed by the two populations. And while the breadth of information we gained from using otolith microchemistry would not have been possible with conventional tagging techniques, this approach was imperfect.

We were unable to use assignment methods (e.g., Muhlfeld et al. 2012; Wolff et al. 2012; Brennan et al. 2015a) to confidently assign a single natal stream of origin or region to each fish. Assignment methods are most useful when one can identify a single stream or region of origin to infer migration pathways. We were unable to do this because we were working at a small spatial scale that had large overlap in surface water strontium signatures among tributaries (Ciepiela and Walters 2019). As a result, we took a conservative approach to building a candidate list of probable source locations for each fish. Our assignment model allowed us to obtain high assignment accuracy (the true stream of origin made the candidate list 100% of the time) but at the cost of precision (one to eight streams of origin made the candidate list). By achieving high assignment accuracy, we could confidently conclude where fish were **not** coming from, which was needed for eliminating potential spawning tributaries for each species and assessing straying rates of spawning rainbow trout.

Although our assignment approach was unable to assign a fish to a single stream or region of origin, our approach and newer geographically continuous assignment approaches (e.g., Wunder 2010; Brennan and Schindler 2017) provide a transparent way to estimate the resolution, and thus precision, that movement and origin of mobile species can be inferred. These assignment methods inherently limit the resolution of inferred origin and movement to the resolution afforded by the environmental tracer, a distinct advantage over nominal approaches, which require a priori determination of isotopic groups.

While many studies that use otolith microchemistry have successfully traced natal origins to specific tributaries, low assignment precision is not unusual for otolith microchemistry studies, especially for studies conducted in small watersheds (Gahagan et al. 2012). In watersheds where assignment precision is low, the ability to draw inferences on migration and origin is often limited. Our approach of comparing the otolith strontium isotope ratio distribution, and thus habitat use, within and between populations provides a novel and promising approach to investigate migration variation between populations. Our method, which is a visual representation of habitat use, allowed us to look at broader-scale differences in habitat use between species. This approach is particularly beneficial where identifying precise and accurate environmental history is not possible due to overlapping surface water environmental signatures.

### Conclusions

An overwhelming body of literature has indicated migration diversity in anadromous salmonids is tightly linked to population resiliency (see Schindler et al. 2010; Waldman et al. 2016). Our results suggest, like anadromous salmonids, inland salmonid populations can express both high inter- and intraspecific migration diversity. As such, we expect identifying and maintaining inland salmonid migration variants will be an important conservation strategy for propagating resilient populations in not only the UNPR fishery, but in impaired and thriving inland salmonid populations alike.

### Author's contributions

Both authors contributed to the conception and design of the study; L.C. collected and analyzed the data; both authors contributed critically to the drafts and gave final approval for publication.

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