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Life history structure of westslope cutthroat trout: Inferences from otolith microchemistry

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ABSTRACT

Life history diversity is important for population stability and is dependent on connectivity to habitat that supports all life stages and life history strategies for a species. Westslope Cutthroat Trout *Oncorhynchus clarkii lewisi* (WCT) exhibit plasticity in life history strategies in response to environmental variability, but fisheries managers have been challenged with evaluating the life history structure of WCT populations. The goals of this research were to use strontium isotopes (i.e., $^{87}Sr/^{86}Sr$) derived from ambient water and sagittal otoliths to assess spatial variability and describe the life history structure of WCT. Water samples (n = 49) and WCT (n = 571) sagittal otoliths were collected throughout the Coeur d'Alene Lake basin in Idaho and analyzed for Sr isotopes. Model-based discriminant function analysis was used to assign WCT to natal tributaries and to infer maternal origins. Life history structure was inferred from maternal signatures and indicated that fluvial (68% of all fish), resident (27%), and adfluvial (5%) life history strategies were present. Connectivity in lotic systems and from lotic to lentic environments supports WCT life history diversity and contributes to a broad distribution of the species.

1. Introduction

Understanding habitat connectivity in relation to life history diversity has been a challenge in managing migratory fishes (Schlosser, 1991; Fausch et al., 2002; Wells et al., 2003). Westslope Cutthroat Trout[1] *Oncorhynchus clarkii lewisi* (WCT) are known to exhibit life history strategies (i.e., fluvial, adfluvial) involving migration (Bjornn and Mallet, 1964; Liknes and Graham, 1988; Varley and Gresswell, 1988; Behnke, 1992). Therefore, WCT movements in aquatic systems are temporally and spatially dependent on connectivity to habitat that supports all life stages and life history strategies (Bjornn and Mallet, 1964; Schmetterling, 2001; Young, 2011). Life history diversity in WCT populations has likely contributed to their broad distribution in the U. S. and Canada (Behnke, 1992; Shepard et al., 2005). However, populations of WCT have declined in their historical distribution because of anthropogenic disturbances that reduced connectivity, such as dams (Schmetterling, 2003), timber harvest (Hicks et al., 1991), livestock grazing (Peterson et al., 2010), and water temperature (Dobos et al., 2016). As a result, Westslope Cutthroat Trout populations have been the focus of fisheries investigations because they have experienced a loss of connectivity throughout their native distribution due to habitat degradation (Bjornn and Mallet, 1964; Meehan, 1991; Brown and Mackay, 1995; Schmetterling, 2001; Shepard et al., 2005; Young, 2011; Muhlfeld et al., 2012). Quantifying the effects that a loss of connectivity has on life history diversity and population viability is important, but difficult. Research that used conventional tracking methods, for example, radiotelemetry (Brown and Mackay, 1995; Schmetterling, 2001), tagging (Quinn and Fresh, 1984), trapping (Apperson et al., 1988), and genetic markers (Wirgin et al., 1995) lacked the ability to evaluate the life history of wild fishes over long time periods (i.e., the life of a fish). Furthermore, a comprehensive evaluation of the life history structure of a fish population should include adults and juveniles from that population. Using unique chemical signatures derived from fish otoliths provides us with the information to investigate the life histories of fish in multiple age classes, and subsequently evaluate the life history structure of a population. Research using elemental

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[1] Westslope Cutthroat Trout *Oncorhynchus clarkii lewisi* (WCT) Laser ablation multicollector inductively coupled plasma mass spectrometry (LA-MC-ICP-MS) Thermal ionization mass spectrometry (TIMS)

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chemistry in otoliths to evaluate connectivity in marine habitats has been established (Gillanders, 2005), but investigating the influence of connectivity on life history diversity using otolith microchemistry in freshwater systems is a new approach. This study used otolith microchemistry to investigate how connectivity to multiple waterbodies influences life history diversity in a WCT population.

Otolith microchemistry has emerged as a powerful tool for evaluating the life histories of fishes and the subsequent life history diversity in fish populations (Campana and Thorrold, 2001; Kennedy et al., 2002; Wells et al., 2003; Barnett-Johnson et al., 2008; Muhlfeld et al., 2012; Benjamin et al., 2014). Analyzing otoliths for trace elements and stable isotopes has been used for inferring migration history, life history variation, maternal origins, stock assessment, and natal origins of freshwater and marine fishes (Campana, 1999; Volk et al., 2000; Kennedy et al., 2002; Bacon et al., 2004; Barnett-Johnson et al., 2008; Muhlfeld et al., 2012; Pracheil et al., 2014). Isostructural to calcium (Ca), strontium (Sr) replaces Ca in geological and biological structures. Therefore, concentrations of Sr, that reflect the geology of a drainage, are incorporated into the calcified otoliths of fish. The transgenerational inheritance of stable isotopes is well established such that it has been used as a mass-marking tool for the offspring of female fishes (Thorrold et al., 2006; Zitek et al., 2013; Starrs et al., 2014). For example, ions are transferred from the blood plasma of a female fish into her eggs that are developing in her ovaries and are consequently inherited into the fluid of a yolk sac (Kalish, 1990; Campana, 1999; Volk et al., 2000; Campana and Thorrold, 2001; Barnett-Johnson et al., 2008). Therefore, as otoliths develop prior to hatching they reflect the chemical signatures of the mother (Kalish, 1990; Volk et al., 2000; Zimmerman and Reeves, 2002; Munro et al., 2009; Zitek et al., 2013; Hegg et al., 2018). A larval fish absorbs the yolk sac and subsequently inherits the chemical signatures from its mother in its otoliths. If the mother lived in a different water chemistry than where the eggs hatch, then the larvae will retain the chemical signature of her previous location (Volk et al., 2000; Bacon et al., 2004). Investigating maternal origins using otolith chemistry has been conducted on anadromous (Volk et al., 2000; Bacon et al., 2004; Hegg et al., 2018) and partially anadromous (Courter et al., 2013; Veinott et al., 2014) fish populations. In the current study, we investigated the life history structure of a wild, non-anadromous, freshwater salmonid fish population using maternal and natal signatures derived from otolith chemistry.

Westslope Cutthroat Trout is a coldwater salmonid native to western North America (Behnke, 1992; Shepard et al., 2005). In the Spokane River basin of northern Idaho, WCT are native upstream of Spokane Falls in Coeur d'Alene Lake and its tributaries (Behnke, 1992). Westslope Cutthroat Trout occupy a variety of coldwater habitats varying from high-elevation, low-productivity, headwater streams to highly productive, large rivers (Rieman and Apperson, 1989; Behnke, 1992; Shepard et al., 2005; Sloat et al., 2005). Two major life history forms characterize the WCT subspecies: migratory (i.e., fluvial, adfluvial) and nonmigratory (i.e., resident; Behnke, 1992; Northcote, 1997; Schmetterling, 2001; Muhlfeld et al., 2009). All life history strategies contain mobile life stages at some spatial and temporal scale. Furthermore, multiple life history strategies are often demonstrated in the same watershed (Bjornn and Mallet, 1964; Behnke, 1992; Gresswell et al., 1994). Because WCT can demonstrate multiple life history strategies in a single lotic-lentic system (Bjornn and Mallet, 1964; Behnke, 1992; Northcote, 1997; Shepard et al., 2005; Muhlfeld et al., 2009), it is important to understand the population structure using adults and juveniles so that conservation and management actions are effective and efficient.

Life history strategies of WCT have been studied in the Coeur d'Alene Lake basin since 1961 when Averett (1962) investigated the age, growth, and behavior of migratory and nonmigratory WCT. Migratory and nonmigratory life history forms of WCT were further observed in the St. Joe, Coeur d'Alene, and St. Maries river watersheds, and in direct tributaries of Coeur d'Alene Lake (Averett, 1962; Thurow and Bjornn, 1978; Rieman and Apperson, 1989; DuPont et al., 2004; Wells et al., 2003; Parametrix, 2006). Additional Coeur d'Alene Lake tributaries were surveyed for adfluvial WCT presence; migratory and resident life history forms were observed in Wolf Lodge Creek and in Benewah and Lake creeks on the Coeur d'Alene Indian Reservation (Firehammer et al., 2012). Thurow and Bjornn (1978) concluded that there were both migratory and resident stocks of WCT in St. Joe River tributaries. Previous research that investigated the life history structure of WCT in the Coeur d'Alene Lake basin used tagging (Horton and Mahan, 1988), radio telemetry (DuPont et al., 2004; Parametrix, 2006; Firehammer et al., 2012), passive integrated transponder (PIT) tagging (Firehammer et al., 2012), netting (Averett, 1962), and trapping (Horton and Mahan, 1988; Apperson et al., 1988; Firehammer et al., 2012). A previous study investigated the validity of using hard-part chemistry to describe movements of WCT in the Coeur d'Alene River basin (Wells et al., 2003). Wells et al. (2003) found that otoliths could be used to describe movements of WCT through the Coeur d'Alene River basin due to heterogeneous geology and the stability of the water chemistry.

Although the St. Maries River has not been the focus of extensive research, nor is it annually monitored by the Idaho Department of Fish and Game (IDFG), there has been investigation into WCT migratory behavior in the St. Maries River basin. Distribution studies (Apperson et al., 1988; Horton and Mahan, 1988) and radio telemetry (Parametrix, 2006) have been used to evaluate WCT in the St. Maries River basin. Sample sizes in the radio telemetry study were small ($n = 17$ fish tagged in the lower St. Maries River) and tracking was limited, but migratory movement patterns were observed (Parametrix, 2006). Notably, a higher proportion of fish tagged in the St. Maries River moved downstream and out of the system than fish tagged in the Coeur d'Alene and St. Joe rivers. Downstream movement patterns are an exhibition of fluvial and adfluvial migration behavior (Bjornn and Mallet, 1964; Thurow and Bjornn, 1978; Knight et al., 1999; Muhlfeld et al., 2009; Firehammer et al., 2012; Campbell et al., 2018). Previous research on WCT in the Coeur d'Alene Lake basin suggests that movement among lotic systems and between lotic-lentic environments contributed to a broad distribution and to the persistence of WCT populations. However, where population linkages exist and the extent to which WCT use the Coeur d'Alene Lake basin at-large is mostly unknown. Furthermore, there is a knowledge gap pertaining to the life history structure of the WCT population in the St. Maries River basin, and whether adfluvial WCT use the St. Maries River basin and contribute to the Couer d'Alene Lake WCT population. Identifying locations in the St. Maries River basin that promote life history diversity and recruitment of WCT is imperative for creating a holistic management approach.

The introduction of nonnative fishes, hybridization, overharvest, habitat loss, and habitat degradation have contributed to losses of connectivity and ultimately a reduction of WCT distribution throughout Idaho and western North America (Allendorf and Leary, 1988; Rieman and Apperson, 1989; Behnke, 1992; Schmetterling, 2001; Northwest Power and Conservation Council, 2005; Shepard et al., 2005; Muhlfeld et al., 2009). These limiting factors affect fish populations in freshwater and marine systems, but our study used techniques that can be applied in other systems to understand life history diversity and connectivity of migratory fish populations. In this study, we collected WCT and water samples throughout the Coeur d'Alene Lake watershed and its sub-basins in northern Idaho. We analyzed water samples and otoliths for Sr isotope ratios (i.e., $^{87}Sr/^{86}Sr$). In conjunction with sampling fish, we conducted habitat assessments in the St. Maries River basin at multiple spatial scales. Our objectives were to (*i*) assess spatial variability of various waterbodies throughout the Coeur d'Alene Lake watershed and its sub-basins, (*ii*) use maternal signatures derived from primordia of otoliths to infer the life history structure of the WCT population in the St. Maries River basin, and (*iii*) investigate relationships between habitat characteristics and life history strategy (i.e., resident, fluvial, adfluvial) of WCT in St. Maries River tributaries.

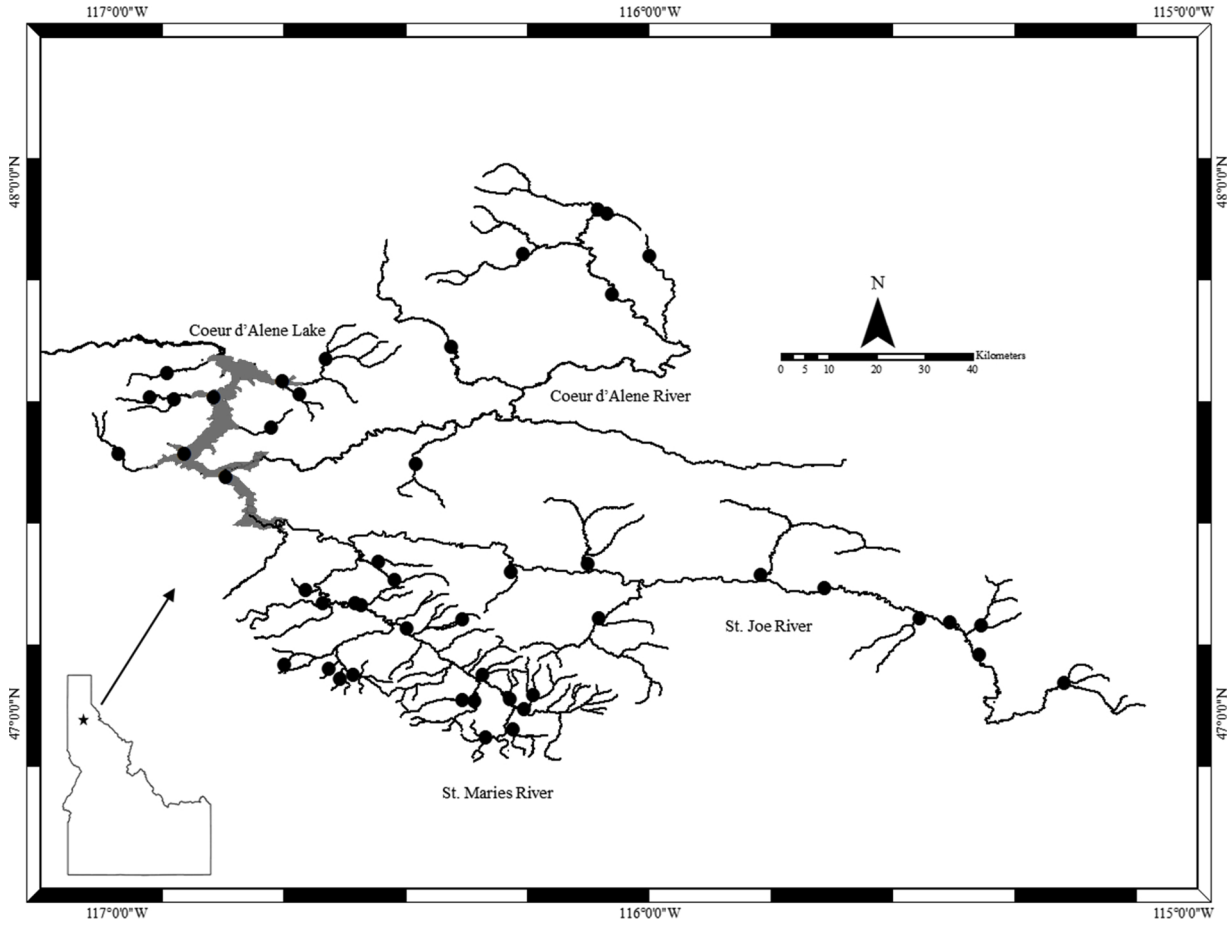

Fig. 1. Locations where water samples and age-0 Westslope Cutthroat Trout were collected in 2016 and 2017 are symbolized by black circles. Map data are from the National Hydrography Dataset, U. S. Geological Survey.

2. Methods

2.1. Study area

The Coeur d'Alene Lake basin is located in the panhandle of Idaho and drains an area of approximately 9946 km^2 (Fig. 1; Northwest Power and Conservation Council, 2005). The basin extends from the Bitterroot Divide along the Montana-Idaho border in the east to the outlet (i.e., Spokane River) of Coeur d'Alene Lake in the west. Elevations vary from 646 m at the lake to over 2134 m along the Bitterroot Divide. Coeur d'Alene Lake is a glacially-formed, natural lake. The only outflow is the Spokane River, which is dammed at Post Falls, Idaho. Post Falls Dam is privately owned and operated by Avista Corporation. Approximately 27 tributaries flow into Coeur d'Alene Lake; the two principle tributaries are the Coeur d'Alene River and the St. Joe River. The Coeur d'Alene River drains an area of approximately 3900 km^2 with around 75 major tributaries. The St. Joe River drains approximately 4500 km^2 with about 75 tributaries. The St. Maries River is a sixth-order tributary of the St. Joe River that joins the St. Joe River about 25 km upstream from Coeur d'Alene Lake. The St. Maries River basin drains an area of approximately 1800 km^2, extends into four counties (Benewah, Clearwater, Latah, and Shoshone), and is characterized by alluvial sedimentary deposits resulting from the formation of ancient Lake Clarkia (Ladderud et al., 2015). The geology in the St. Maries River basin is diverse, which lends to variability in the underlying geology among drainages in the system. The St. Maries River contains 26 major drainages. Elevations in the St. Maries River basin vary from approximately 670 m to 1600 m, and the mainstem St. Maries River has a longitudinal elevation difference of 207 m. The Coeur d'Alene and St. Joe rivers support popular recreational fisheries for WCT, whereas the St. Maries River does not receive as much effort from anglers. A variety of native fishes occupy the St. Maries River basin, including Westslope Cutthroat Trout *Oncorhynchus clarkii lewisi*, mountain whitefish *Prosopium williamsoni*, northern pikeminnow *Ptychocheilus oregonensis*, longnose dace *Rhinichthys cataractae*, speckled dace *Rhinichthys osculus*, redside shiner *Richardsonius balteatus*, bridgelip sucker *Catostomus columbianus*, largescale sucker *Catostomus macrocheilus*, shorthead sculpin *Cottus confusus*, and torrent sculpin *Cottus rhotheus*. Additionally, nonnative fishes occupy the watershed, including brook trout *Salvelinus fontinalis*, brown bullhead *Ictalurus nebulosus*, pumpkinseed *Lepomis gibbosus*, and tench *Tinca tinca*.

2.2. Water sampling

In 2016 and 2017, we collected water samples throughout the Coeur d'Alene Lake basin and its sub-basins (i.e., Coeur d'Alene, St. Joe, St. Maries river basins; Fig. 1) to characterize isotopic (i.e., $^{87}Sr/^{86}Sr$) variability within and among watersheds. Water samples were taken during baseflow periods at the downstream end of a sampling reach to characterize the interaction between water and geology. Vials (50 ml polypropylene), lids, and syringes (10 ml polypropylene) used for water sampling were acid-washed, rinsed with ultrapure water, air dried, and then stored in sterile Whirl Paks (Nasco, Fort Atkinson, Wisconsin). Water was filtered through 25 mm diameter, 2 µm nylon syringe filters (GE, Pittsburgh, Pennsylvania). Water samples were analyzed for $^{87}Sr/^{86}Sr$ isotope ratios using inductively coupled plasma mass spectrometry (ICP-MS) at the University of California-Davis Interdisciplinary Center for Plasma Mass Spectrometry (UC-Davis), and

using thermal ionization mass spectrometry (TIMS) at the University of Idaho Kennedy LIFE Lab – TIMS Laboratory. Replicate analysis of the National Institute of Standards and Technology standard reference material (SRM-987) was used to standardize analytical equipment and estimate error.

2.3. Fish and habitat sampling

In 2016, backpack electrofishing was used to collect WCT from streams throughout the Coeur d'Alene Lake watershed and its sub-basins. Sampling in 2016 was conducted as a "proof of concept" to evaluate whether otolith chemistry was a viable technique for this study. Sites (n = 43) were predetermined and selected based on where previous research sampled WCT (Fig. 1; Apperson et al., 1988; Wells et al., 2003; Ryan et al., 2013). An emphasis on collecting age-0 WCT and water samples were the focus in 2016 to assess isotopic variability and evaluate if otolith microchemistry could be used to infer life history structure of WCT caught in the Coeur d'Alene Lake watershed. Fishes were sampled in each reach using single-pass pulsed direct current (PDC) electrofishing (Model LR-24 Backpack Electrofisher; Smith Root, Inc., Vancouver, Washington; Simonson and Lyons, 1995). For all backpack electrofishing, two netters each used a 6.4 mm mesh dip net to collect fishes. Seconds of electrofishing were recorded for each macrohabitat. Electrofishing continued in each stream until 10 age-0 WCT were caught. Westslope Cutthroat Trout were sacrificed, frozen, sagittal otoliths were extracted and prepared for microchemistry analysis in the lab, and age was estimated. In addition to collecting WCT, hook-and-line sampling was conducted on Coeur d'Alene Lake in 2016 (n = 4 sites) to collect kokanee *Oncorhynchus nerka*, which served as a surrogate when water samples were compared to otoliths.

Gill netting was conducted on Coeur d'Alene Lake in October 2017 to collect WCT from the lake and obtain a lake signature from WCT otoliths. Floating gill nets were 45 m long and 1.8 m deep. Each net consisted of 6 panels; each panel was 7.6 m long and designed from smallest to largest mesh size (i.e., 1.9, 2.5, 3.2, 3.8, 5.1, 6.4 cm bar-measure). Nets were set for a total of 134 net nights. All WCT caught were sacrificed, measured for total length (TL; mm), and weight was measured to the nearest tenth of a gram. Sagittal otoliths were extracted and transferred to the laboratory where they were prepared for microchemistry analysis, and age was estimated.

In 2017 and 2018, sampling was focused in the St. Maries River basin from March through August. From March through mid-May, the mainstem St. Maries River was sampled using drift boat electrofishing, then tributaries of the St. Maries River were sampled using backpack electrofishing from mid-May through August. The mainstem St. Maries River was sampled from March through May to coincide with WCT migrations to spawning tributaries (Averett, 1962; Apperson et al., 1988; Firehammer et al., 2012). The St. Maries River is approximately 76 km long from the mouth to the town of Clarkia where the Middle Fork St. Maries River and Merry Creek join. The St. Maries River was divided into three large sections based on access limitations. River sections were defined as the lower river, extending from the mouth upstream to the confluence with Santa Creek; the middle river, from the confluence with Santa Creek upstream to the town of Fernwood; and the upper river, from the town of Fernwood upstream to the confluence with Merry Creek.

The St. Maries River was further subdivided into 1 km reaches (n = 76) and sampling occurred in a 1-in-2 systematic design. A 1 km sampling reach was randomly selected from the first two 1 km reaches and sampling began at the upstream boundary of the respective reach. Each subsequent 1 km sampling reach was 1 km downstream from the previous reach, such that every other river kilometer was sampled in a section. Starting and ending points of sampling reaches were flagged and georeferenced with a handheld global positioning system (GPS; GPSMAP 64 st; Garmin, Olathe, Kansas). Some reaches were sampled more than once in a field season. One section of river, approximately 22 km long, was not sampled due to unsafe whitewater conditions. In 2017, 58 reaches were sampled. In 2018, 34 reaches were sampled. Fewer reaches were sampled in 2018 due to large, woody obstructions that blocked the entire river and prevented boat passage.

Sampling the St. Maries River was accomplished by using a 4 m long, low-sided drift boat (Koffler Boats, Eugene, Oregon). Water temperature (°C) and conductivity (μS/cm) were taken prior to active electrofishing using a handheld probe (DiST, Hanna; Woonsocket, Rhode Island). Pulsed direct current power was provided by a 5000 W generator and standardized to 2,750-3,250 W based on water conductivity (Miranda, 2009). Electricity was applied to the water using an Infinity model electrofisher (Midwest Lake Management, Inc., Polo, Missouri). Electrofishing began at the uppermost point of the sampling reach and proceeded in a downstream direction. One netter was positioned at the bow of the boat and used a 2.4 m long dip net with 6 mm bar knotless mesh. Although the focus was to collect WCT, all fishes were netted and placed into an aerated live well until the entire reach was sampled. All fishes were identified to species and measured for TL to the nearest mm. Up to 10 WCT per 10-mm length-group were sacrificed, sagittal otoliths were extracted and prepared for microchemistry analysis, and age was estimated. Weight was measured from sacrificed WCT to the nearest tenth of a gram. Minutes of active electrofishing were recorded for each reach and were used to calculate catch-per-unit-effort ([CPUE] = fish/minute of electrofishing).

Fishes were sampled from tributaries in the St. Maries River basin in 2017 and 2018 in conjunction with habitat assessments (Fig. 2). A stratified sampling design was used to select the locations of sampling reaches. Tributaries of the St. Maries River were considered strata and reaches were randomly selected in each stratum. Reaches varied in length based on the average wetted stream width (Lyons, 1992; Simonson and Lyons, 1995) and were selected using a random point generator in ArcMap version 10.5.1 (Esri, Redlands, California). In 2017, sampling was conducted from May–August on 44 reaches in 33 different tributaries. In 2018, sampling was conducted from June–August on 24 reaches in 20 different tributaries. Water temperature (°C) and conductivity (μS/cm) were taken prior to electrofishing using a handheld probe (DiST, Hanna; Woonsocket, RI). Fishes were sampled in each reach using single-pass PDC electrofishing (Model LR-24 Backpack Electrofisher; Smith Root, Inc., Vancouver, Washington; Simonson and Lyons, 1995). For all backpack electrofishing, two netters each used a 6.4 mm mesh dip net to collect fishes. Seconds of electrofishing were recorded for each macrohabitat and were used to calculate catch-per-unit-effort ([CPUE] = fish/minute of electrofishing). All fishes were identified to species and measured for TL to the nearest mm. The abundance of WCT was variable among reaches, therefore a subsample between 5 and 10 WCT per reach were sacrificed, sagittal otoliths were extracted and prepared for microchemistry analysis, and age was estimated. Weight was measured on sacrificed WCT to the nearest tenth of a gram.

Large-scale habitat characteristics (i.e., gradient, elevation, road density, stream order, land use, geology) were estimated at the basin-level using ArcMap and Terrain Navigator Pro (Version 9.1, MyTopo; Billings, Montana; Meyer et al., 2003; Sindt et al., 2012). Elevation, gradient, and stream order were estimated from USGS Topographic Maps at 1:24,000 scale using Terrain Navigator Pro. The distance (m) between the two contour lines that bounded the sampling reach was traced. Gradient was calculated as the elevational increment (12.192 m) between those two contour lines divided by the traced distance (Meyer et al., 2003). Distance to road (m), road density, and geology were estimated using ArcMap. Road density was calculated as kilometers of roads per square kilometer (km/km^2; Vadal and Quinn, 2011). Geology was determined from the USGS mineral resources Idaho geologic map geospatial dataset (ArcMap 10.5.1, Redlands, California). Dominant land use was determined in the field and categorized as timberland, land that had recently been or was currently being clear cut for timber; mineral, land that was managed and used for mineral

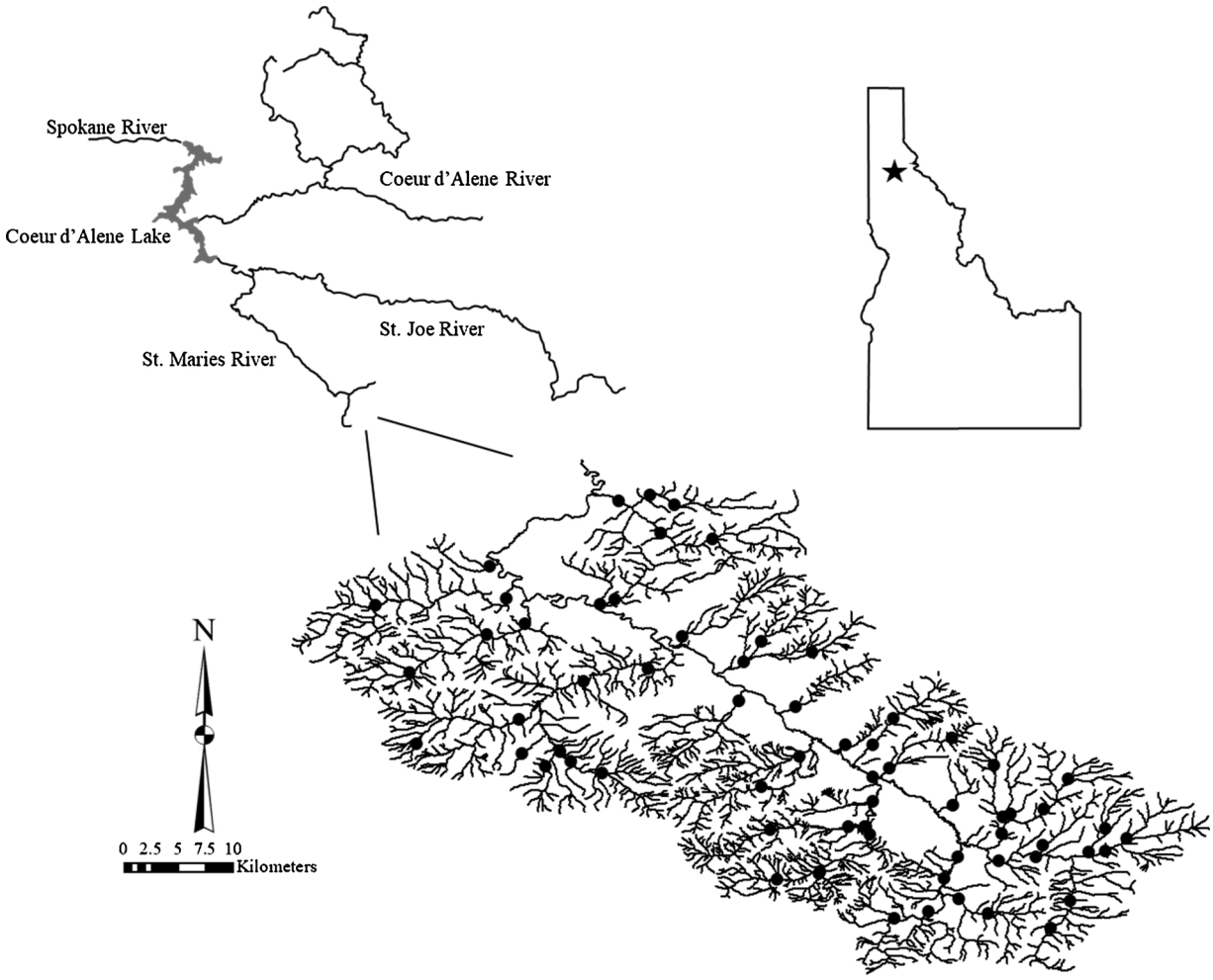

Fig. 2. Tributary sites where sampling was conducted in 2017 and 2018 in the St. Maries River basin are symbolized by black circles. Map data are from the National Hydrography Dataset, U. S. Geological Survey.

extraction; private property, residential homes or summer camps; cattle-grazed, land where cattle grazing was occurring; forest, land that did not have noticeable effects from timber harvest; and thinned forest, forests that were not clear cut, but had some timber harvested. All instream cover at least 0.3 m in length and in water 0.2 m deep or greater was quantified by taking one length measurement, three width measurements, and three depth measurements. Instream cover was classified as undercut bank, overhanging vegetation, branch complex, log complex, root wad, boulder, rip-rap, or aquatic vegetation (Quist et al., 2003).

2.4. Otolith preparation and analysis

After sagittal otoliths were extracted from WCT, otoliths were wiped clean of any tissue and stored dry in 1.5 ml polypropylene vials. One otolith per fish was mounted with the sulcus acusticus side facing up onto a glass cover slide, then mounted onto a microscope slide using Crystalbond 509-3 (Aremco, Valley Vintage, New York). Mounted otoliths were wet-sanded using ultrapure water on a Buehler MetaServ 250 (Buehler, Lake Bluff, Illinois) with 600–1200 grit silicon carbide sandpaper. Otoliths were sanded until daily growth increments from the primordium (i.e., prehatch region) to the dorsal and ventral edges were exposed (Thorrold et al., 1998; Hobbs et al., 2010; Chase et al., 2015). A compound microscope was used in conjunction with sanding to assess progress. Otoliths on glass cover slips were then removed from the microscope slide and remounted onto petrographic slides with Crystalbond for laser ablation multicollector inductively coupled plasma mass spectrometry (LA-MC-ICP-MS).

Otoliths were analyzed for Sr isotopes using LA-MC-ICP-MS at UC-Davis using a New Wave Research UP213 (Fremont, California) laser ablation system coupled with a Nu Plasma HR (Nu032; North Wales, United Kingdom) multiple-collection, high-resolution, double-focusing plasma mass spectrometer system. Line scans were ablated from the ventral edge, through the primordium, to the dorsal edge to generate a $^{87}Sr/^{86}Sr$ profile throughout the life of each fish. Line scans were programmed from edge-to-edge because it provided more data per sample and isotopic shifts at the primordium were more distinguishable compared to programming scans from either the primordium to the edge or programming spot scans. The line scan distance (μm) from otolith edge to the primordium and total line scan distance were recorded. The measurement from otolith edge to the primordium was also used to estimate the location of the maternal signature at the primordium during data analysis (Kalish, 1990; Volk et al., 2000; Zimmerman and Reeves, 2002; Bacon et al., 2004). Settings for line scans included a scanning speed of 5 μm/s, beam width of 40 μm, laser pulse frequency of 10 Hz, and 60% laser power were used. Values for the $^{87}Sr/^{86}Sr$ isotope ratio were normalized for instrumental mass discrimination by monitoring the $^{86}Sr/^{88}Sr$ isotope ratio (assumed $^{86}Sr/^{88}Sr = 0.1194$). The interference of rubidium (^{87}Rb) on the $^{87}Sr/^{86}Sr$ isotope ratio was corrected by monitoring the ^{85}Rb signal. Instrumental accuracy and precision were evaluated by analyzing a white seabass *Atractoscion nobilis* otolith before and after each sample slide of WCT otoliths. To compare analysis days, values for $^{87}Sr/^{86}Sr$ derived from WCT otoliths were normalized in each session based on the correction factor of the

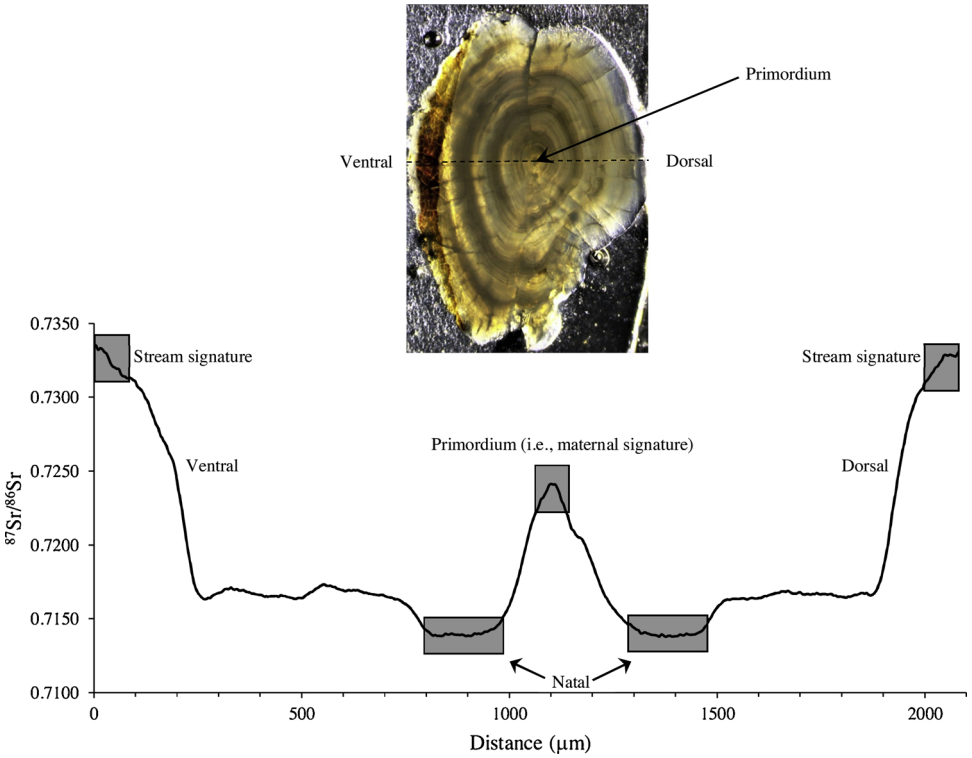

Fig. 3. Digital image of a sagittal otolith from a Westslope Cutthroat Trout with line scan (dashed line) from laser ablation and the corresponding output of reduced data as a line plot. Regions of the reduced data that were used for maternal, natal, and stream signatures are highlighted in gray boxes.

White Seabass otolith (mean $^{87}Sr/^{86}Sr = 0.709098$, SD = 0.000075, $n = 89$) to the modern seawater value of $^{87}Sr/^{86}Sr$ (0.70918; McArthur et al., 2001).

2.5. Data analysis

Data reduction and analysis of WCT otoliths were conducted using the IsoFishR app in R Statistical Software (Willmes et al., 2018; R Core Development Team 2018). Data were reduced at an integration time of 0.2 s, blank time of 30 s, minimum ^{88}Sr value set to 0.2 V, and maximum ^{88}Sr set to 9.95 V. Data were smoothed to a ten-point moving average for visual inspection and outliers > 2 SD were removed (Chase et al., 2015). Data were further analyzed by manually selecting visible differences in heterogeneous samples (Fig. 3) then summary statistics (i.e., mean, standard deviation) were calculated for each region (Willmes et al., 2018). Plots of reduced data were used to visually inspect each otolith and identify regions of maternal, natal, and stream signatures. The mean for two different regions (i.e., maternal, stream) were calculated for each otolith of WCT caught in St. Maries River tributaries. Means for three different regions (i.e., maternal, natal, stream) were calculated for each otolith of WCT caught in the St. Maries River. The maternal signature was estimated visually by referring to plots of reduced data in IsoFishR. To confirm that the maternal signature was at the primordium, we referenced the measurement that was recorded when line scans were programmed. Maternal signatures were derived from the area within the hatch check at the primordium (Volk et al., 2000; Bacon et al., 2004). Natal signatures were estimated from the area immediately adjacent to the maternal signature where stable $^{87}Sr/^{86}Sr$ isotope ratios occurred (Barnett-Johnson et al., 2005). Due to variability in the ages of WCT and subsequently the sizes of otoliths, a standard distance from the primordium to where natal regions were derived was unavailable. Stream signatures were estimated using the chemistry of the dorsal and ventral edges of each otolith from regions of stable $^{87}Sr/^{86}Sr$ (Brennan et al., 2015). Otolith edges contained the area of most recent otolith growth and were assumed to represent the stream of capture. In addition to using $^{87}Sr/^{86}Sr$ isotope ratios, ^{88}Sr values (measured in volts) were also derived from the same regions of each otolith to further discriminate among locations. There was low variability in ^{88}Sr values among samples collected from each stream, which is why we chose to include ^{88}Sr coupled with $^{87}Sr/^{86}Sr$. Therefore, each WCT otolith had unique values of $^{87}Sr/^{86}Sr$ and ^{88}Sr for each life stage.

Stream signatures derived from otoliths of all WCT collected per stream were pooled and summary statistics (i.e., mean, standard deviation, standard error) were calculated. Each stream was assigned a stream signature based on $^{87}Sr/^{86}Sr$ values from otoliths and was then compared to $^{87}Sr/^{86}Sr$ values from water samples. Linear regression was conducted to evaluate the relationship between ambient water and stream signatures derived from otoliths (Bath et al., 2000; Kennedy et al., 2000; Barnett-Johnson et al., 2008; Muhlfeld et al., 2012; Brennan et al., 2015). Normality tests were conducted to assess the variance structure of $^{87}Sr/^{86}Sr$ from water samples and showed that assumptions of normality were violated. Therefore, nonparametric Kruskal-Wallis and post-hoc pairwise comparisons tests ($\alpha = 0.05$) were conducted to compare $^{87}Sr/^{86}Sr$ from water samples among watersheds of the Coeur d'Alene Lake basin (Dunn, 1964). The {dunn.test} package in R (Dinno, 2017) was used to conduct post hoc pairwise comparisons and *P*-values were adjusted for multiple comparisons by controlling the false discovery rate using the Benjamini and Hochberg (1995) adjustment.

Model-based discriminant function analysis (DFA) was conducted using the {Mclust} package in R (Fraley and Raftery, 2002; Scrucca et al., 2016) to determine whether $^{87}Sr/^{86}Sr$ and ^{88}Sr values from otoliths could assign WCT from the St. Maries River to natal streams and to infer the maternal origins of WCT caught in St. Maries River tributaries. The {Mclust} package provides alternatives to traditional linear discriminant function that assumed observations to be multivariate normal (Fraley and Raftery, 2002). Discriminant analysis was based on Gaussian finite mixture modeling fitted by the expectation maximization (EM) algorithm that allowed for different covariance structures and different numbers of mixture components within groups.

Table 1
Habitat variables for 68 stream reaches in 35 different tributaries of the St. Maries River collected in 2017–2018. Variables were used as independent variables in logistic regression models to investigate the relationship between habitat characteristics and Westslope Cutthroat Trout life history strategy (SD = standard deviation; min = minimum; max = maximum).

Variable	Description	Mean	SD	Min	Max
Elevation	Elevation (m) of the upstream end of the stream reach	891.10	94.34	671.00	1302.00
Gradient	Reach length divided by the elevation change (%)	2.30	1.40	0.39	7.30
Road Density	Kilometers of roads per square kilometer (km/km^2)	1.42	0.56	0.42	2.51
Distance to road	Distance to the nearest road (m)	308.64	529.28	3.58	3096.42
Temperature	Mean stream temperature (°C)	13.45	2.52	7.03	19.58
Proportion Cover	Proportion of reach with instream cover	0.23	0.15	0.00	0.51
BKT Presence	Percentage of reaches where Brook Trout occurred	29.00	46.00	0.00	100.00
Stream order	Strahler (1964) stream order	4.00	1.12	1.00	5.00
Land use	Grazing, mineral, private, thinned forest, timberland				
Geology	Basalt, meta-argillite, mica-schist, siltstone				

Stream signatures (i.e., $^{87}Sr/^{86}Sr$, ^{88}Sr) from known capture locations were used as the training data set, then unknown locations of natal and maternal signatures were classified (Thorrold et al., 1998; Barnett-Johnson et al., 2008). The proportion of each life history strategy (i.e., resident, fluvial, adfluvial) was estimated in tributaries. Maternal signatures were used to infer the population structure of WCT in St. Maries River tributaries and evaluate where production from adfluvial fish was occurring. Discriminant function models were further tested using K-fold cross validation to investigate classification accuracy (Fraley and Raftery, 2002; Scrucca et al., 2016). We used 25 folds because there were 25 groups (i.e., tributaries) in the training data set. Logistic regression was conducted to investigate the relationship between habitat characteristics (Table 1) and life history strategy (Hosmer and Lemeshow, 1989). Life history strategy (i.e., resident, fluvial, adfluvial) was the categorical dependent variable and habitat characteristics served as independent variables. For all covariates that had a significant effect ($\alpha = 0.05$) on life history strategy, the predicted probabilities were plotted to further evaluate the covariate.

3. Results

Water sample ($n = 49$) $^{87}Sr/^{86}Sr$ signatures varied significantly among the basins of Coeur d'Alene Lake ($\chi^2 = 29.97$, df = 4, $P < 0.01$; Fig. 4). Post-hoc pairwise comparisons indicated that water sample $^{87}Sr/^{86}Sr$ signatures from the St. Maries River basin were significantly different from the St. Joe River ($P < 0.01$) and Coeur d'Alene Lake ($P = 0.02$), but not from Coeur d'Alene Lake tributaries ($P = 0.58$) or tributaries in the Coeur d'Alene River basin ($P = 0.96$). In the St. Maries River basin, there was no significant difference in water sample $^{87}Sr/^{86}Sr$ signatures among tributary reaches ($\chi^2 = 17$, df = 17, $P = 0.45$). The relationship between water sample $^{87}Sr/^{86}Sr$ signatures and otolith $^{87}Sr/^{86}Sr$ signatures were highly correlated ($r^2 = 0.98$; Fig. 5; Table 2).

A total of 46 WCT ($n = 46$ for microchemistry analysis) was caught in Coeur d'Alene Lake and varied in TL from 190 to 480 mm (Fig. 6) and the average TL was 308 ± 73 mm (mean ± standard deviation [SD]). Ages of WCT caught in Coeur d'Alene Lake varied from 1 to 12 years. Westslope Cutthroat Trout were distributed throughout the St. Maries River basin at multiple spatial scales. In the mainstem of the St. Maries River, 92 reaches were sampled in 2017 and 2018. In total, 125 WCT ($n = 99$ for microchemistry analysis) were sampled from 55 reaches (60%) in the mainstem of the St. Maries River. Average TL of WCT caught in the St. Maries River was 297 ± 74 mm (range, 151–477 mm). Ages of WCT caught in the St. Maries River varied from 1 to 12 years. In tributaries of the St. Maries River basin, 652 WCT ($n = 418$ for microchemistry analysis) were sampled from 52 reaches (76%) out of 68 reaches in 35 different tributaries and ages varied from 0 to 5 years. Total length of WCT varied from 23 to 406 mm and averaged 110 ± 57 mm. Unlike water samples, $^{87}Sr/^{86}Sr$ stream signatures derived from otoliths were significantly different ($\chi^2 = 401.76$, df = 24, $P < 0.01$) among St. Maries River drainages. Additionally, the isotope ^{88}Sr provided further discriminatory power among St. Maries River tributaries (Fig. 7).

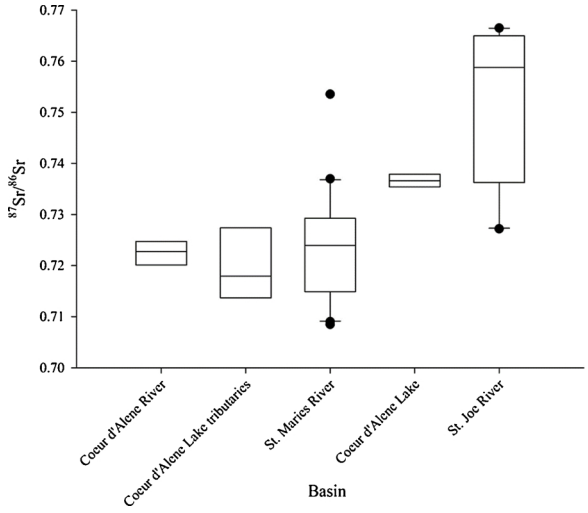

Fig. 4. Spatial variability in $^{87}Sr/^{86}Sr$ values from water samples collected in 2016 and 2017 from the Coeur d'Alene River basin ($n = 7$), Coeur d'Alene Lake tributaries ($n = 7$), the St. Maries River basin ($n = 20$), Coeur d'Alene Lake ($n = 4$), and the St. Joe River basin ($n = 10$).

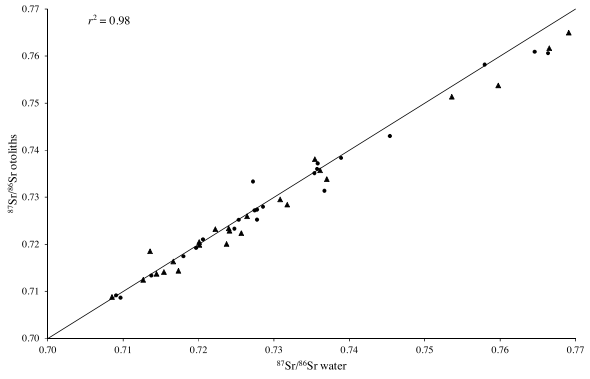

Fig. 5. The linear relationship of $^{87}Sr/^{86}Sr$ ratios in water to otolith edge samples from Westslope Cutthroat Trout collected from 16 tributaries of the St. Maries River, 3 locations in the St. Maries River, 6 tributaries of the St. Joe River, 4 locations in the St. Joe River, 5 tributaries of the Coeur d'Alene River, 7 tributaries of Coeur d'Alene Lake, and from 4 locations in Coeur d'Alene Lake. The solid line represents a 1: 1 relationship between water and otolith values. Solid circles (●) represent waters samples analyzed using MC-ICPMS and solid triangles (▲) represent waters samples analyzed using TIMS.

Table 2
Locations where water samples and Westslope Cutthroat Trout samples were collected in 2016–2018 to obtain $^{87}Sr/^{86}Sr$ isotope ratios. Sample size (n) and the mean of all samples from each location were used to estimate the stream signature from the edge of otoliths. The standard error (SE) of the mean is included and the corresponding water sample $^{87}Sr/^{86}Sr$ signature from locations where water samples were taken.

Basin	Stream	*n*	Otolith edge mean	SE	ICP-MS water sample	SE	TIMS water sample	SE
Coeur d'Alene River	Independence Creek	5	0.724564	0.000845	—	—	—	—
	Jordan Creek	5	0.719905	0.000061	—	—	0.720103	0.000001
	Latour Creek	6	0.725269	0.000095	0.725300	0.000007	—	—
	Little N. F. Coeur d'Alene	3	0.723402	0.000162	0.724726	0.000007	—	—
	N. F. Coeur d'Alene$_{middle}$	0	—	—	0.722883	0.000004	0.722770	0.000002
	N. F. Coeur d'Alene$_{upper}$	0	—	—	0.723769	0.000007	—	—
	Shsoshone Creek	8	0.719292	0.000111	0.719626	0.000006	—	—
	Tepee Creek	5	0.721089	0.000077	0.720562	0.000010	—	—
Coeur d'Alene Lake	Coeur d'Alene Lake$_{north}$	10	0.735315[a]	0.000210	0.735190	0.000005	—	—
	Coeur d'Alene Lake$_{midnorth}$	8	0.735684[a]	0.000154	0.736064	0.000005	—	—
	Coeur d'Alene Lake$_{midsouth}$	5	0.735786[a]	0.000228	0.737254	0.000007	—	—
	Coeur d'Alene Lake$_{south}$	4	0.735411[a]	0.000421	0.738722	0.000005	0.738131	0.000001
	Coeur d'Alene Lake$_{WCT}$	46	0.731417[b]	0.000405	0.736660[c]	0.000647	—	—
	Beauty Creek	11	0.727452	0.000098	0.727712	0.000006	—	—
	Benewah Creek	8	0.714723	0.001390	—	—	—	—
	Bozard Creek	5	0.713784	0.000049	—	—	—	—
	Carlin Creek	12	0.727282	0.000058	0.727395	0.000005	—	—
	Cougar Creek	10	0.717506	0.000033	0.717942	0.000005	—	—
	E. F. Bozard Creek	1	0.714325	0.000000	—	—	—	—
	Lake Creek	7	0.718548	0.000123	0.713564	0.000007	0.713564	0.000002
	N. F. Mica Creek	5	0.716399	0.000031	—	—	0.716622	0.000002
	S. F. Mica Creek	9	0.713393	0.000046	0.713692	0.000005	—	—
	Wolf Lodge Creek	8	0.720998	0.000155	0.721143	0.000004	—	—
St. Maries River	Alder Creek	4	0.714392	0.000368	0.717353	0.000006	0.717315	0.000002
	Beaver Creek	1	0.719673	0.000000	—	—	—	—
	Blair Creek	3	0.725045	0.000316	—	—	—	—
	Canyon Creek	40	0.708708	0.000093	0.709610	0.000005	—	—
	Carlin Creek	22	0.712493	0.000035	—	—	0.712642	0.000001
	Carpenter Creek	4	0.733041	0.000123	—	—	—	—
	Cat Spur Creek	25	0.720544	0.000218	—	—	0.720047	0.000005
	Charlie Creek	1	0.725980	0.000000	—	—	0.726402	0.000007
	Childs Creek	34	0.733907	0.000612	—	—	0.736991	0.000002
	Corbett Creek	11	0.728216	0.000441	—	—	—	—
	Crystal Creek	1	0.733190	0.000000	—	—	—	—
	Davis Creek	4	0.738873	0.000198	—	—	—	—
	E. F. Charlie Creek	2	0.729569	0.000260	—	—	0.730793	0.000002
	E. F. Emerald Creek	9	0.722910	0.001348	—	—	0.724074	0.000001
	Flat Creek	26	0.708836	0.000432	—	—	0.708490	0.000002
	Flewsie Creek	15	0.720479	0.000141	—	—	—	—
	Gold Center Creek	7	0.719549	0.000259	—	—	—	—
	Gramp Creek	5	0.728865	0.000789	—	—	—	—
	Hume Creek	14	0.720137	0.000541	—	—	0.723686	0.000002
	John Creek	2	0.712608	0.000029	—	—	—	—
	Little E. F. Emerald Creek	5	0.723929	0.000762	—	—	—	—
	Merry Creek	25	0.730248	0.000298	—	—	—	—
	Middle Fork St. Maries River	26	0.723253	0.000215	—	—	0.722219	0.000004
	Olson Creek	12	0.735347	0.000578	—	—	—	—
	Renfro Creek	15	0.742896	0.002008	—	—	0.753555	0.000002
	S. F. Santa Creek	17	0.713752	0.000043	—	—	0.714395	0.000002
	St. Maries River$_{lower}$	1	0.722388	0.000000	0.725588	0.000006	0.725653	0.000002
	St. Maries River$_{middle}$	22	0.725302	0.001049	0.727726	0.000005	—	—
	St. Maries River$_{upper}$	76	0.723402	0.000308	—	—	0.723966	0.000001
	Thorn Creek	34	0.709237	0.000047	0.709020	0.000005	—	—
	W. F. Emerald Creek	10	0.728447	0.000923	—	—	0.731750	0.000005
	W. F. Merry Creek	21	0.735754	0.000302	—	—	0.736095	0.000002
	W. F. St. Maries River	31	0.714128	0.000241	—	—	0.715369	0.000001
St. Joe River	Big Creek	5	0.733402	0.000158	0.727195	0.000009	—	—
	Bluff Creek	5	0.755894	0.001280	—	—	0.759718	0.000002
	Gold Creek	5	0.765027	0.001232	—	—	0.769090	0.000002
	Hugus Creek	4	0.738430	0.000231	0.738867	0.000006	—	—
	Marble Creek	10	0.728023	0.000193	0.728498	0.000005	—	—
	N. F. St. Joe River	7	0.743110	0.000428	0.745328	0.000006	—	—
	St. Joe River$_{lower}$	5	0.762304	0.000621	0.766226	0.000006	0.766495	0.000002
	St. Joe River$_{middle}$	5	0.760460	0.000489	0.766300	0.000012	—	—
	St. Joe River$_{upper}$	10	0.760288	0.000761	0.764536	0.000005	—	—
	St. Joe River$_{headwaters}$	11	0.758252	0.002008	0.757916	0.000007	—	—
Total		773						

[a] signatures derived from kokanee otoliths.
[b] signatures derived from WCT otoliths.
[c] average of water samples from Coeur d'Alene Lake.

The direct error rate of the training dataset used to assign WCT to natal streams was 19%, which means 81% of samples were correctly assigned when the training dataset was run through the discriminant function. The cross-validation error rate for the natal assignment dataset was 40% (i.e., 40% misclassified). Westslope Cutthroat Trout caught in the St. Maries River were assigned to a natal tributary in the St. Maries River basin (Fig. 8). Although WCT were caught in all sections of the St. Maries River, most natal signatures (69%) were assigned to tributaries in the upper St. Maries River basin (i.e., upstream of Clarkia). A second set of training data that included the Coeur d'Alene Lake $^{87}Sr/^{86}Sr$ and ^{88}Sr signatures was used to estimate the maternal origins of WCT that were caught in tributaries and infer population structure. The DFA for estimating maternal origins was 73% accurate (i.e., direct error rate of the training set) at correctly classifying known origin fish (Fig. 9). The cross-validation error rate for the maternal origins dataset was 46% (i.e., 46% misclassified). Most (68%) maternal origins were estimated to originate in the St. Maries River basin from locations other than the tributary where the sampled fish was caught. Fish that did not assign to the stream where they were captured, or Coeur d'Alene Lake, were deemed to have a fluvial mother. Fish that had a maternal signature estimated to originate from the stream where they were captured (27%) were deemed to have a resident mother. A portion (5%) of maternal origins were estimated to originate from Coeur d'Alene Lake and these fish were deemed to have an adfluvial mother. To infer life history structure, the proportion of each life history strategy was estimated in St. Maries River tributaries (Fig. 10). Although the adfluvial life history strategy was estimated to be the smallest proportion in the watershed, adfluvial signatures were most prevalent in tributaries located in the northeast portion of the basin. Tributaries that drained the northeast portion of the St. Maries River basin contained the greatest number ($n = 16$) of adfluvial maternal signatures compared to tributaries in the upper ($n = 4$) and southwest ($n = 2$) regions of the basin.

Results from logistic regression models did not indicate that habitat characteristics had a significant effect on predicting whether a fish would be adfluvial. There were no obvious patterns in habitat that were observed in tributaries with adfluvial signatures. The distance (km) of a drainage to the mouth of the St. Maries River, stream order, and gradient had significant effects on whether a fish was fluvial or resident (Table 3). For example, as the distance from the mouth of the St. Maries River to a drainage increased the likelihood of a fish having a fluvial maternal signature also increased. No covariates had a significant effect on predicting whether a fish was adfluvial.

4. Discussion

Previous studies have used trace elements and isotopic ratios in otoliths to reconstruct the life histories of anadromous fishes (Kennedy et al., 2002; Hobbs et al., 2007; Barnett-Johnson et al., 2008; Hegg et al., 2013; Brennan and Schindler, 2017) and using the technique in freshwater systems has become more prevalent (Wells et al., 2003; Pangle et al., 2010; Muhlfeld et al., 2012; Chase et al., 2015). Two such studies (Wells et al., 2003; Muhlfeld et al., 2012) investigated using trace elements to evaluate the validity of using otolith microchemistry in freshwater systems to determine the migratory behavior of WCT. Both studies discriminated among locations where fish were sampled at multiple spatial scales based on heterogeneity in geology and stream water chemistry. Furthermore, microchemistry analyses conducted on otoliths showed that otoliths consistently represented water chemistry where they lived and that fish movements in freshwater could be inferred from changes in chemical signatures in otoliths. The current study expanded on previous microchemistry research by using a larger sample size, inferring life history structure from Sr isotopes in otoliths, investigating where production of various life history strategies occurred using maternal and natal assignments, related life history strategy to habitat characteristics, and inferred the importance of connectivity to life history diversity. In addition, results from the current study were not only investigative, but the motivation behind a large sample size at this spatial scale was to inform fishery managers where recruitment was occurring for resident, fluvial, and adfluvial WCT in the St. Maries River basin. The observed life history diversity in the St. Maries River basin suggests that connectivity from tributaries to the mainstem river and to Coeur d'Alene Lake exists and has contributed to population viability. Our methods can be applied to other freshwater systems where scientists are studying the influence of connectivity on life history diversity and systems where the life history structure of a fish population is unknown.

The relationship between $^{87}Sr/^{86}Sr$ from water samples and WCT otoliths was representative of the relationship between water and otoliths reported in previous studies (Kennedy et al., 2000; Barnett-Johnson et al., 2008; Muhlfeld et al., 2012; Brennan et al., 2015). Due to the high correlation between Sr isotopes in water and otoliths, we could use either water samples or otoliths to assess spatial variability. However, because there were similarities in the underlying geology in the Coeur d'Alene Lake basin, some watersheds (i.e., Coeur d'Alene, St. Maries rivers) exhibited similar $^{87}Sr/^{86}Sr$ stream signatures. Therefore, using Sr isotopes alone to discriminate among watersheds in the Coeur d'Alene Lake basin for the purpose of assigning lake-caught WCT to their natal origins could lead to high rates of misclassification. We

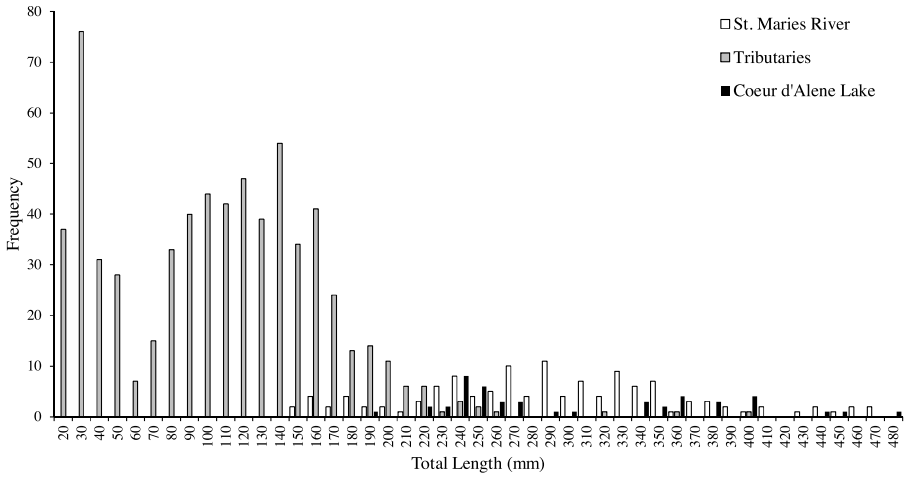

Fig. 6. Comparison of the distribution of length frequencies of Westslope Cutthroat Trout sampled in the mainstem ($n = 99$) of the St. Maries River, tributaries ($n = 418$) of the St. Maries River, and Coeur d'Alene Lake ($n = 46$).

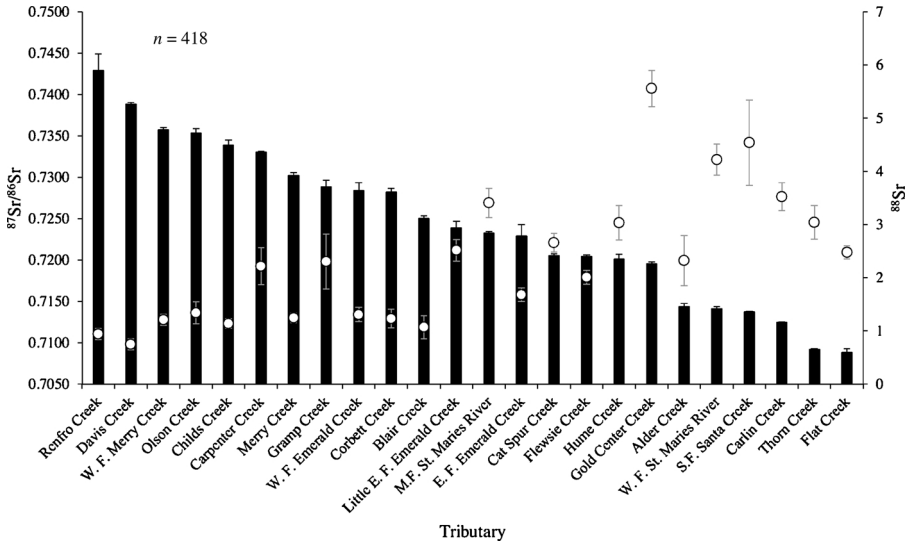

Fig. 7. Values of $^{87}Sr/^{86}Sr$ (black bars) and ^{88}Sr (white circles) derived from Westslope Cutthroat Trout sagittal otoliths that were caught in St. Maries River tributaries. Error bars represent one standard error of the mean.

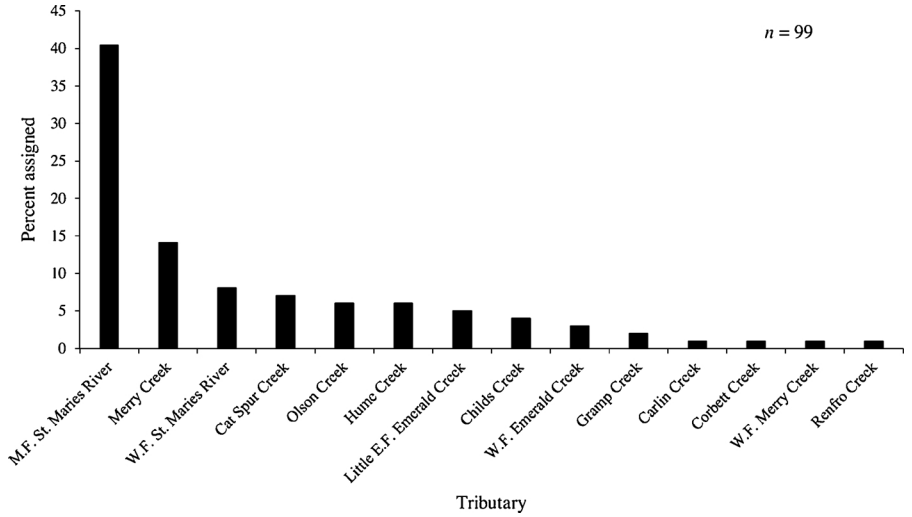

Fig. 8. The percent of Westslope Cutthroat Trout of unknown natal origin assigned to each tributary based on natal signatures from fish caught in the St. Maries River. Discriminant function analysis was used to assign fish to natal tributaries.

observed high rates of misclassification in our cross validation error rates for assigning maternal origins and natal origins. Using a combination of $^{87}Sr/^{86}Sr$ and ^{88}Sr improved our classification accuracy, but we never achieved 90% or greater accuracy in our cross validation. Measuring other elemental ratios (e.g., Mg/Ca, Ba/Ca; Wells et al., 2003; Clarke et al., 2007; Hobbs et al., 2007; Macdonald et al., 2008) in addition to Sr isotopes could provide better classification accuracy in Coeur d'Alene Lake sub-basins that had similar Sr isotope signatures. We recommend analyzing otoliths for multiple elemental ratios in future studies to improve classification accuracy.

Referring to the primordium region of otoliths to make inferences about maternal origins has predominately focused on anadromous fishes (Kalish, 1990; Volk et al., 2000; Donohoe et al., 2008; Miller and Kent, 2009; Hegg et al., 2018). Additionally, it has been suggested that maternal signatures may have some influence from spawning streams based on the extent of migration to spawning tributaries and the duration of spawning (Donohoe et al., 2008; Hegg et al., 2018). In the current study, substantial heterogeneity in Sr isotopes among tributaries, the mainstem of the St. Maries River, and Coeur d'Alene Lake provided enough spatial variability to infer the maternal origins of juvenile WCT in a freshwater system and characterize population structure at the drainage and watershed scales. Line scans ablated across the sagittal plane of otoliths revealed migration histories or residency of WCT throughout a freshwater system. Furthermore, line scans in the current study encompassed otolith growth from dorsal to ventral edge including the primordium, which provided more data at the primordium where the maternal signature was derived compared to line scans measured from the otolith core to the edge. Owing to the migratory behavior of some WCT, the characteristics of transgenerational inheritance of Sr into eggs (Kalish, 1990; Volk et al., 2000; Thorrold et al., 2006; Zitek et al., 2013; Starrs et al., 2014), and heterogeneity in geology, we were able to delineate differences between maternal, natal, and stream regions of otoliths. With the ability to differentiate between regions of otoliths, we established that there was a relationship between where natal and maternal signatures were assigned. This overlap in assignment was evidence of life history diversity and that recruitment occurred for resident, fluvial, and adfluvial fish in tributaries. Although some maternal signatures were assigned to Coeur d'Alene Lake, the proportion of adfluvial WCT using the St. Maries River basin was likely underestimated in this study. However, results from the current study support that it is possible to infer life history structure using maternal signatures of a freshwater salmonid in a

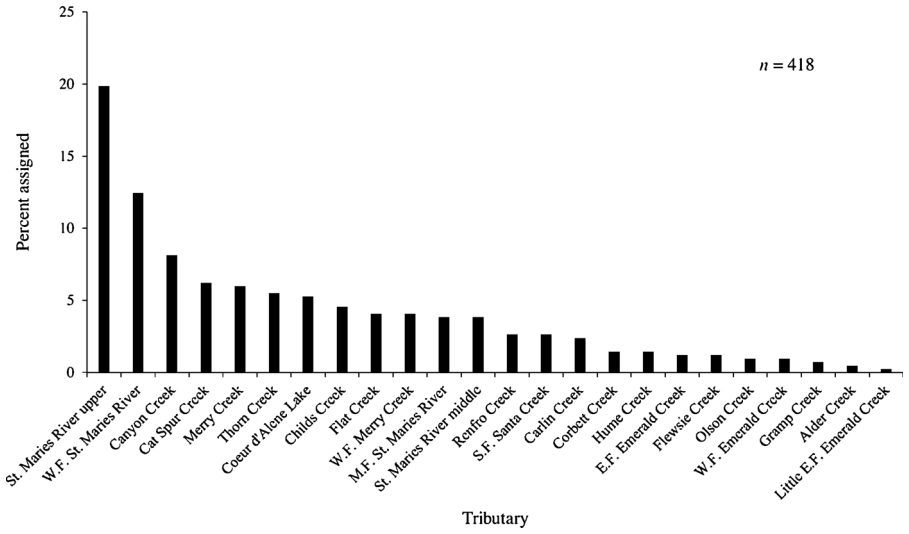

Fig. 9. The percent of Westslope Cutthroat Trout of unknown maternal origin assigned to each location based on maternal signatures from fish caught in St. Maries River tributaries. Discriminant function analysis was used to assign the maternal origins of Westslope Cutthroat Trout.

heterogeneous environment using Sr isotopes. Our techniques could be used in other freshwater systems to answer similar research questions.

Westslope Cutthroat Trout are known to exhibit multiple life history strategies in a single watershed (Bjornn and Mallet, 1964; Behnke, 1992; Northcote, 1997; Shepard et al., 2005; Muhlfeld et al., 2009). Although the DFA did not assign WCT with 100% accuracy, patterns in life history structure at multiple spatial scales emerged and WCT in the St. Maries River basin displayed substantial life history diversity. Westslope Cutthroat Trout populations are often robust in headwater streams and the upper portions of watersheds (Shepard et al., 2005). In the St. Joe River, Thurow and Bjornn (1978) hypothesized that fluvial and resident life history strategies were more dominant farther upstream from Coeur d'Alene Lake. Our results in the neighboring St. Maries River corroborate these results. For example, most natal and maternal signatures were assigned to the upper portion of the basin near Clarkia, Idaho. Additionally, the results from our logistic regression analyses indicated fish were more likely to be fluvial migrants farther upstream from the river mouth. This pattern suggests that the upper watershed has adequate habitat throughout the year and can support all life stages of WCT. In addition to adequate habitat, it may be

Table 3
Habitat variables for 68 stream reaches in 35 different tributaries of the St. Maries River collected in 2017–2018 to investigate the relationship between habitat characteristics and westslope cutthroat trout life history strategy. Variables that had a significant ($\alpha = 0.05$) effect on life history strategy responses (SE = standard error). Coefficient estimates are the log odds of the response variable. For example, for a one-unit increase in river kilometer distance from the mouth of the St. Maries River, the log odds of a fish being resident decreases by 0.11.

Variable	Coefficient estimate	SE	*P* value
Resident response			
River km	−0.11	0.02	< 0.01
Stream order	−0.50	0.23	0.03
Gradient	−0.52	0.16	< 0.01
Fluvial response			
River km	0.09	0.02	< 0.01
Stream order	0.52	0.20	0.01
Gradient	0.45	0.14	< 0.01

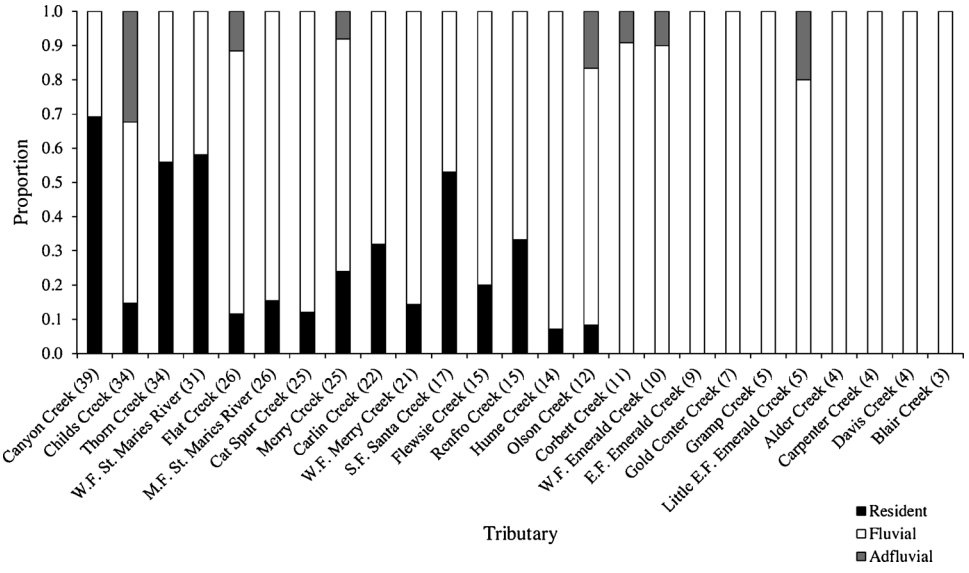

Fig. 10. The life history structure of Westslope Cutthroat Trout ($n = 418$) in St. Maries River tributaries. Life history structure was estimated from maternal signatures from fish that were caught in tributaries. Tributaries are ranked by sample size (n) from greatest to smallest. For example, Canyon Creek had the greatest number of samples ($n = 39$) used for microchemistry analysis and the dominant life history strategy expressed was resident. About 70% of samples from Canyon Creek had a maternal signature assigned back to Canyon Creek.

energetically more costly for WCT to migrate downstream and back to Coeur d'Alene Lake than to remain in the upper river system, which may substantiate why the fluvial life history strategy was the dominant strategy observed in the watershed. Additionally, connectivity to suitable habitat and resources for adult WCT in the St. Maries River basin is evident by similar length structures of WCT sampled in the St. Maries River to WCT sampled in Coeur d'Alene Lake—the assumption being that adfluvial WCT would grow to larger sizes by migrating as juveniles to Coeur d'Alene Lake and maturing in the lake, rather than residing as juveniles in the St. Maries River to maturity. A wider range of feeding opportunities and temperatures are available in lakes, thus we assumed that adfluvial WCT would be larger in the Coeur d'Alene Lake system. However, movement downstream and out of the St. Maries basin was not essential for WCT to grow to large body size. Rather, WCT could achieve large body size and remain in the St. Maries River watershed because there was connectivity to resources in the basin to support large, adult WCT. However, the inability of WCT to achieve greater sizes in Coeur d'Alene Lake than in the St. Maries River may indicate that abiotic or biotic factors in the lake are affecting growth of WCT.

The number of fish estimated to have an adfluvial mother in St. Maries River tributaries was low (i.e., 5% of total), which could have affected our observations relating life history form to habitat characteristics. Most adfluvial signatures were detected in fish sampled from the northeast portion of the watershed, which was also characterized by high-gradient tributaries. However, gradient was significantly related to the fluvial and resident life history forms and not the adfluvial form. Fish that emigrated from a tributary could have encountered suitable habitat between their natal tributary and Coeur d'Alene Lake, hence the correlation between an increase in gradient to a greater likelihood that a fish would be fluvial and not adfluvial. No significant relationship was observed between the adfluvial life history form and the distance from the river mouth to a drainage. Our explanations for this observation are that (*i*) a migration to the St. Maries River basin from Coeur d'Alene Lake may be too energetically costly for fish to make, (*ii*) there may be suitable spawning tributaries closer to Coeur d'Alene Lake in which offspring have greater survival and the migratory distance is shorter, and (*iii*) our sampling distribution may not have encountered enough locations to collect adfluvial fish. Although there were no relationships between habitat characteristics and the adfluvial life history strategy, connectivity within the St. Maries watershed and to the lake was observed and migration distances were within the potential home range size of WCT.

Home range size has been shown to average about 65 km and vary from 7 to 235 km in a fluvial WCT population (Schoby and Keeley, 2011). Results from the current study indicated that adfluvial WCT influence in the St. Maries River basin is slight even though the distance from the mouth of the St. Maries River to Coeur d'Alene Lake is about 25 km. The distance from the mouth of the St. Maries River upstream to the first tributary (i.e., Flat Creek) where an adfluvial signature was detected was 34 km from the river mouth, a total distance of approximately 59 km from Coeur d'Alene Lake. About 86 km upstream from Coeur d'Alene Lake is Childs Creek, which was where the highest proportion (32%) of adfluvial maternal signatures were observed. An additional caveat to the maternal signature assignments from Childs Creek to Coeur d'Alene Lake is that 6% of samples were misclassified to Coeur d'Alene Lake instead of Childs Creek. Nonetheless, the pattern of adfluvial fish production occurring in the tributary is still evident. Considering the potential home range size of WCT, the distance from Coeur d'Alene Lake to St. Maries River spawning tributaries falls within the home range size of what has been described for the species.

Life history structure of WCT was characterized at multiple spatial scales using Sr isotopes obtained from sagittal otoliths. Heterogeneity in water chemistry among tributaries made it possible to infer population structure and expand on previous research (Wells et al., 2003; Muhlfeld et al., 2012) that used otolith microchemistry on WCT. Migratory and nonmigratory life histories were evident in the St. Maries River basin when sagittal otoliths were analyzed from dorsal to ventral edges due to spatial variability in Sr isotopes. The current study provided methodology for analyzing sagittal otoliths for the purpose of understanding the life history and population structure of WCT at multiple spatial scales to inform management decisions. Although the current study used a large sample size at a broad scale and there were similarities in Sr isotopes among tributaries, discriminatory power was retained by using multiple Sr isotopes as markers for each location and each otolith signature. However, there are limitations with using ^{88}Sr as an indicator for stream location. Environmental factors (i.e., water temperature, underlying geology) and unreplicable laboratory conditions (i.e., LA-MC-ICP-MS calibration) can influence how ^{88}Sr is incorporated and analyzed in otoliths. In the current study, there was low variability in ^{88}Sr among samples collected from the same tributaries, but using ^{88}Sr as a unique identifier for stream location should be done with caution.

Life history diversity is important for population stability and hinges on connectivity to habitat that supports all life stages and strategies for a species (Northcote, 1997; Rieman and Dunham, 2000; Moore et al., 2014). Connectivity to a variety of waterbodies creates a pathway for gene flow and decreases the extinction risk of local populations. In response to environmental variability, plasticity in life history can help maintain a population. As anthropogenic disturbances, nonnative species, and habitat alterations continue in aquatic ecosystems, connectivity will be essential to maintain life history diversity, population stability, and prevent local extinctions. Resident, fluvial, and adfluvial life history strategies were observed in the St. Maries River basin, which illustrates the importance of maintaining connectivity to multiple types of habitat to support a diverse population. The St. Maries watershed is an example of the importance of maintaining connectivity to support population viability in response to altered habitat. For example, habitat fragmentation in St. Maries River tributaries resulted from thermal barriers (i.e., water temperature) in late summer, but WCT could move through these barriers during spring to successfully spawn in headwaters and contribute to genetic diversity. The observed diversity in life history structure throughout the St. Maries River basin illustrates that large-scale connectivity exists and promotes population viability. The WCT population in the St. Maries watershed has likely persisted in response to environmental change and land use activities because of life history diversity and connectivity to suitable habitat. Although biotic interactions (e.g., Brook Trout) and poor habitat have decreased the abundance of WCT in some tributaries, the resiliency and wide distribution of WCT in the St. Maries watershed has likely helped maintain the population in response to adverse conditions. Local adaptations of WCT in response to environmental change in the St. Maries River basin has prompted life history diversity and contributed to population stability. This study suggests that connectivity supports life history diversity in a native Cutthroat Trout population. Therefore, when managing a migratory freshwater salmonid it is important to consider the complexity of populations and the role that connectivity plays in life history diversity and population viability.

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