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Population Structure and Movement Dynamics of Redband Trout in the Kootenai River Basin

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ABSTRACT

Redband Trout *Oncorhynchus mykiss gairdneri* is a species of high conservation concern in the Kootenai River basin, United States and Canada. However, identifying the specific mechanisms influencing Redband Trout is difficult as its life history structure is largely unknown. Using otolith microchemistry analysis, we found that 18.5% ($n = 66$) of the fish sampled ($n = 329$) were a product of mainstem Kootenai River spawning. The remainder were fish ($n = 264$) that originated from one of 31 tributaries throughout the basin. Redband Trout were captured between 0 and 153 km from their assigned natal tributaries. Most migratory fish originated from tributaries in the uppermost portion of the study area and had migratory mothers. However, a diversity of life history types (e.g., multi-year resident, migratory) was observed in the population. Redband Trout were estimated to outmigrate from natal habitats at a variety of ages (0–3 years) and lengths (12–430 mm). Our results highlight diversity in the population structure of Redband Trout and provide information valuable to conservation efforts in the Kootenai River system. Interestingly, several tributaries identified as natal habitats of Redband Trout contain substantial obstacles originally considered barriers to upstream fish passage. In addition, some streams in the lower portion of the Kootenai River basin with degraded habitat that were not expected to contribute Redband Trout had natal assignments. These observations indicate previously unknown sources of Redband Trout and support the notion that improved fish passage in disconnected and degraded streams could increase production of Redband Trout throughout the Kootenai River basin. Restoration efforts in the mainstem that include considerations for spawning and natal habitat may also aid in conservation efforts for Redband Trout. Our research demonstrates the value of microchemistry in planning and evaluating habitat restoration to recover fishes in large rivers.

1 | Introduction

Native fishes throughout North America are facing declines in distribution and abundance (Sala et al. 2000; Dudgeon et al. 2006; Darwall and Freyhof 2015). Declines of native fishes stem from a variety of anthropogenic disturbances, particularly changes in climate, interactions with non-native species, and water development (Pringle et al. 2000; Arthington

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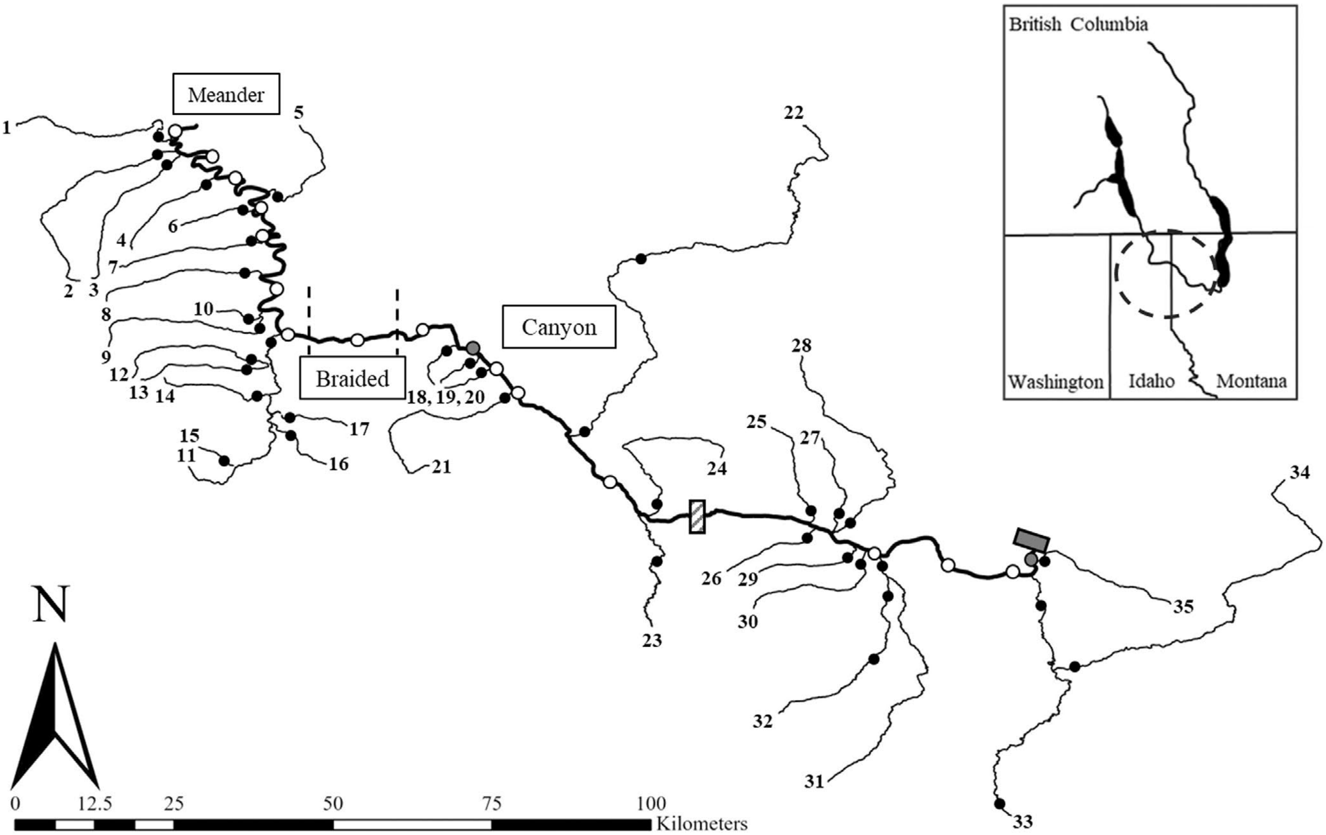

FIGURE 1 | The section of Kootenai River (bold line) and its tributaries (fine lines) included in the current study. Study area spans from Libby Dam (gray box) downstream to the Idaho-British Columbia border. The dashed box marks Kootenai Falls, Montana. Black circles are tributary collection sites for age-0 Redband Trout. Gray circles are sites where both age-0 and unknown-origin Redband Trout were collected from the mainstem Kootenai River, and open circles are sites where only unknown-origin Redband Trout were collected. Age-0 Redband Trout were collected in 2014, and unknown-origin Redband Trout were collected in 2014, 2015, and 2023. Dashed lines denote the approximate division between meander, braid, and canyon habitat reaches. Numbers denote stream ID (see Table 1).

et al. 2016; Toussaint et al. 2016; Anas and Mandrak 2021). Large river systems have been highly altered given their societal importance (e.g., agriculture, navigation, municipal water supply).

Impoundment and channelization are common forms of water development that influence fishes and their habitats (Dynesius and Nilsson 1994; Jurajda 1995; Gregory et al. 2002). Impoundments alter flow regimes with regulated discharge that is typically greater in the winter and lower in the spring when compared to historical regimes and exhibit lower variance (Pringle et al. 2000). Similarly, annual temperature fluctuations are reduced. Impoundment also alters sediment dynamics in river systems. Sediment is trapped in reservoirs, leading to altered streambed morphology downstream of dams (e.g., armoring, downcutting; Poff and Hart 2002). Reduced discharge leads to decreased current velocity and flushing flows that typically remove fine sediment from the substrate. Additionally, reservoirs act as nutrient sinks and can alter food web dynamics in downstream habitats (Stockner et al. 2000). Channelization is another form of water development that is often observed in conjunction with impoundment. Channelized rivers are often deepened and disconnected from the floodplain, thereby reducing habitat complexity (Stoffers et al. 2022) and preventing the influx of nutrients following flooding (Junk et al. 1989).

The effects of impoundment and channelization on native fishes have been extensively documented in the Kootenai River basin, a large regulated system in North America that spans state and international borders (Figure 1). Eight dams have been constructed in the Kootenai River basin (Northcote 1973). The most upstream dam in the Kootenai River is Libby Dam, which was constructed in Montana in 1972 to provide flood control and recreational opportunities. Libby Dam has been monitored for its effects on native fishes since construction (Partridge 1983). The Kootenai River downstream of Libby Dam is often referenced by its three major habitat units: the canyon, braided, and meander reaches (Figure 1; Fosness and Williams 2009; Smith et al. 2016). The canyon reach (river kilometer [RKM] 257-312) has the steepest gradient, largest substrate, and highest average velocity of the three reaches. The braided reach (RKM 246-257) is a transitional area from the canyon to the meander reach with a shallow, braided channel structure. The meander reach (RKM 120-246) is the leveed portion of the river that is characterized by its deep sinuous channel, fine substrate, and low average velocity.

Water development in the Kootenai River has greatly altered river dynamics. Historically, annual peak flows in the Kootenai River removed tributary deltas (Dibrani 2003; Zelch 2003). Libby Dam has eliminated flushing flows in the spring, causing

TABLE 1 | Mean ^{87}Sr:^{86}Sr values obtained from water samples and edge of otoliths collected from Redband Trout of known natal locationin the Kootenai River basin.

Habitat-reach	Waterbody	Stream ID	Water ^{87}Sr:^{86}Sr		Otolith ^{87}Sr:^{86}Sr		
			Mean	SE	Mean	SE	*n*
Mainstem	Kootenai River	—	0.715802	0.00002680	0.7163769	0.001143	12
Canyon	Big Cherry Creek$_{upper}$	32	—	—	0.7461198	0.000039	5
	Big Cherry Creek$_{lower}$	32	0.745026	0.00000531	0.7460198	0.000224	4
	Bobtail Creek	27	0.726247	0.00000666	0.7253026	0.000209	5
	Boulder Creek	21	0.731616	0.00000669	0.7306215	0.000138	8
	Caboose Creek	20	0.733627	0.00000596	0.7316910	0.000158	6
	Cedar Creek	26	0.744749	0.00000884	0.7416667	0.000196	5
	Debt Creek	19	0.737848	0.00000767	0.7355248	0.000080	7
	Dunn Creek	35	0.733687	0.00000597	0.7330843	0.000063	5
	Fisher River$_{upper}$	33	—	—	0.7328694	0.000064	5
	Fisher River$_{lower}$	33	0.733940	0.00000653	0.7344531	0.000156	5
	Flower Creek	30	0.740087	0.00000527	0.7389545	0.000843	5
	Katka Creek	18	0.733600	0.00025000	0.7337101	0.000074	8
	Lake Creek	23	0.735000	0.00100000	0.7354961	0.000530	5
	Libby Creek	31	0.742180	0.00000942	0.7393526	0.000125	4
	Obrien Creek	24	0.736080	0.00000666	0.7337572	0.000242	4
	Parmenter Creek	29	0.745035	0.00000696	0.7445804	0.000245	4
	Pipe Creek	28	0.730949	0.00000649	0.7303078	0.000189	5
	Quartz Creek	25	0.734948	0.00000700	0.7322009	0.000131	5
	Wolf Creek	34	0.744304	0.00000660	0.7432311	0.000101	5
	Yaak River$_{upper}$	22	—	—	0.7353938	0.001508	5
	Yaak River$_{lower}$	22	0.733540	0.00400000	0.7347241	0.000200	9
Meander	Ball Creek	8	0.711030	0.00000603	0.7107883	0.000032	8
	Boundary Creek	1	0.722325	0.00000491	0.7255566	0.000093	6
	Caribou Creek	13	0.711551	0.00000519	0.7113091	0.000026	8
	Cascade Creek	10	0.712949	0.00000670	0.7127156	0.000038	8
	Deep Creek	11	0.714839	0.00000634	0.7140898	0.000165	6
	Dodge Creek	15	0.710443	0.00000606	0.7100695	0.000033	5
	Fischer Creek	6	0.713450	0.00000590	0.7130326	0.000050	7
	Long Canyon Creek	3	0.709425	0.00000590	0.7096372	0.000053	8
	Mission Creek	5	0.728290	0.00000452	0.7294401	0.000078	7
	Myrtle Creek	9	0.710592	0.00000443	0.7104105	0.000079	7
	Parker Creek	4	0.711161	0.00000553	0.7106194	0.000074	8
	Ruby Creek	14	0.711534	0.00000499	0.7115999	0.000030	8
	Smith Creek	2	0.709093	0.00001070	0.7094079	0.000062	4
	Snow Creek	12	0.711344	0.00000717	0.7118680	0.000463	7

(Continues)

Habitat-reach	Waterbody	Stream ID	Water $^{87}Sr:^{86}Sr$		Otolith $^{87}Sr:^{86}Sr$		
			Mean	SE	Mean	SE	*n*
	Trail Creek	16	0.710252	0.00000547	0.7101316	0.000026	8
	Trout Creek	7	0.710928	0.00000499	0.7107981	0.000044	5
	Twenty-mile Creek	17	0.711722	0.00000603	0.7118127	0.000028	8

sediment to accumulate in the mainstem riverbed as well as at tributary mouths. Water temperature in the Kootenai River is also regulated by Libby Dam, with higher water temperatures in the winter and lower temperatures in the summer than observed prior to impoundment (Partridge 1983). Nutrient sequestering at Libby Dam has led to declines in growth for multiple fishes in the basin (Snyder and Minshall 1996; Watkins et al. 2017). Reduced nutrients and primary production downstream of Libby Dam are exacerbated by levees, which have disconnected the floodplain since the early twentieth century (Northcote 1973). Although the effects of channelization have not been directly quantified in the Kootenai River basin, they are well described in other large river systems (Brooker 1985; Jurajda 1995; Peipoch et al. 2015). Channelization disconnects floodplains that include important nursery and refugia habitat and eliminates nutrient input from adjacent wetlands (Junk et al. 1989; Bayley 1995). The cumulative effects of water development in the Kootenai River contributed to the listing of White Sturgeon *Acipenser transmontanus* as endangered under the Endangered Species Act (ESA) in 1994 and the near extirpation of Burbot *Lota lota* (Paragamian 2012; Hardy and Paragamian 2013). A variety of habitat restoration projects have been implemented throughout the Kootenai River basin (e.g., floodplain reconnection, flow mitigation, addition of wood and rocky substrate) to aid in the conservation and recovery of native fishes (Kootenai Tribe of Idaho (KTOI) 2009). Habitat restoration has had mixed effects for native fishes in the Kootenai River. Restoration of side channel habitat in the braided reach expanded the distribution of non-native species, likely because of disturbance caused by construction (Watkins et al. 2015). However, an examination of microhabitat in the braided reach found that habitat restoration increased available shallow, slow current velocity habitat, benefiting multiple native fish species (Branigan et al. 2018). Additionally, KTOI and the Idaho Department of Fish and Game (IDFG) implemented a nutrient addition program in 2005 to increase primary production in the Kootenai River (Hoyle 2012). Macroinvertebrate abundance and biomass have increased because of nutrient addition (Minshall et al. 2014). Nutrient addition has also led to positive responses from native fishes such as Largescale Sucker *Catostomus macrocheilus* and Mountain Whitefish *Prosopium williamsoni* (Watkins et al. 2017; Hardy et al. 2022). However, the response of some native fishes to mitigation, including Redband Trout *Oncorhynchus mykiss gairdneri*, remains unclear.

Redband Trout is a salmonid native to the Columbia River basin that exhibits multiple life history strategies (e.g., resident, fluvial, adfluvial; Behnke 2002). All forms of Redband Trout generally spawn in small headwater tributaries in the spring (Muhlfeld 2002). Redband Trout in the Kootenai River were once abundant and supported culturally important subsistence and recreational fisheries (Paragamian 1995; Walters 2003). Redband Trout was petitioned for listing in the Kootenai River in 1994 under the ESA because of apparent declines in abundance. However, ESA listing of Redband Trout in the Kootenai River was not deemed warranted due to a lack of information at the time (U.S. Office of the Federal Register 1995). Redband Trout in the Kootenai River basin is now considered a species of concern by state agencies in Idaho and Montana. The main factors limiting Redband Trout productivity in the Kootenai River are thought to be barriers to fish movement and changes in food web dynamics associated with reduced nutrients. Barriers to Redband Trout movement are largely due to armored alluvial fans at tributary mouths that have developed in the absence of flushing flows in the Kootenai River and perched culverts at roads and railways (Walters 2005; Dunnigan and Terrazas 2021). Although adult Redband Trout are generally able to access spawning tributaries in the spring, juvenile Redband Trout are thought to become stranded during summer low flows when some tributaries are disconnected from the Kootenai River by the armored alluvial fans (Dibrani 2003; Zelch 2003). Decreased growth of Redband Trout in the Kootenai River has been attributed to changes in food web dynamics as a result of nutrient sequestering at Libby Dam (Hardy et al. 2022). However, identifying the specific mechanisms limiting the growth and survival of Redband Trout in the Kootenai River is difficult as the life history structure of the population is undocumented.

Increased knowledge of Redband Trout life history structure can provide insight as to how fish use and move through the environment at different life stages and may help identify recruitment bottlenecks. However, examining the life history structure of Redband Trout in the Kootenai River is difficult due to the size and complexity of the basin. The Kootenai River basin is large (>45,000 km^2), and fish move between multiple state and national jurisdictions. Monitoring population structure using traditional techniques (e.g., tagging, telemetry) is extremely labor and resource intensive, particularly in large watersheds. Otolith microchemistry analysis has been identified as a suitable tool to examine life history structure in large rivers (Clarke et al. 2007; Hegg et al. 2015; Crook et al. 2017). Otoliths consist of calcium carbonate and organics and grow incremental layers throughout the life of a fish. Furthermore, they are metabolically inert and thus capture a lifelong record of growth and environmental conditions (Campana 1999; Whitledge 2017). In particular, the ratio of strontium isotopes ($^{87}Sr:^{86}Sr$) is often used to analyze fish movement in freshwater systems (Avigliano et al. 2020; Cook and Bourret 2022; Dunnigan et al. 2023). This is based on the principle that $^{87}Sr:^{86}Sr$ in freshwater varies among rivers based on differences in the age and composition of the geologic strata of their watershed, and this ratio is incorporated into the otolith layers without significant fractionation (Kennedy et al. 2000; Barnett-Johnson et al. 2008; Pracheil et al. 2014).

Previous studies on salmonids have described maternal, natal, and migratory life history patterns using otolith microchemistry (Kennedy et al. 2002; Barnett-Johnson et al. 2008; Donohoe et al. 2008; Chase et al. 2015; Heckel et al. 2020). Knowledge of location-at-age can be used to infer a fish's life history and potential influences of migration timing, as well as inform growth patterns based on location (Bourret et al. 2014; Ciepiela and Walters 2019; Dunnigan et al. 2023).

The overall goal of this research was to increase our understanding of the life history structure of Redband Trout in the Kootenai River using microchemistry analysis of otoliths. Using ^{87}Sr:^{86}Sr values from known-origin Redband Trout, we created predictive models to identify important natal tributaries and describe differences in the contribution of different streams to the population throughout the Kootenai River basin. This allowed us to evaluate the use of tributaries that were assumed to have barriers to fish passage during low-flow periods. We then identified the maternal life history of each fish sampled to identify connectivity between resident and migrant phenotypes. We then paired microchemistry analysis with age and growth information to detect the timing of outmigration. Using natal tributary assignments and capture information, we also described minimum dispersal distances to provide insight into how fish move in the Kootenai River basin throughout their lifetime. The results of this research provide insight into the life history of Redband Trout that can be used to develop and evaluate conservation actions.

2 | Methods

2.1 | Study Area

The Kootenai River originates in eastern British Columbia, Canada, and flows south into Montana, United States (Figure 1). Near Libby, Montana, the Kootenai River turns northwest and continues through Idaho, then north, returning to British Columbia where it flows into Kootenay Lake. From Kootenay Lake, the Kootenai River continues west to its confluence with the Columbia River at Castlegar, British Columbia. Kootenay Lake was formed over 10,000 years ago, after which fishes in the Kootenai River basin were isolated by natural barriers at Bonnington Falls, British Columbia, and Kootenai Falls, Montana (Northcote 1973; Hildebrand et al. 1999). Corra Linn and Libby dams define the distribution of Redband Trout in this study (Figure 1). Corra Linn Dam is located at the outlet of Kootenay Lake at the former location of Bonnington Falls. Libby Dam is located 50 km upriver from the natural barrier at Kootenai Falls and is the most upstream dam in the Kootenai River.

Strontium isotope tracing depends on heterogeneous geology to discriminate between aquatic habitats (Kennedy et al. 2000; Hegg et al. 2013). The Kootenai River basin is comprised of four major mountain ranges (Horton 2017). The geologic history of the Purcell, Salish, and Cabinet mountains began during the Mesoproterozoic, about 1000–1600 Ma. The Selkirk Mountains of the western basin began forming during the Cretaceous Period between 145 and 66 Ma. Kootenay Lake is influenced by the inflow from the Kootenai River and surrounding tributaries that drain from diverse geologic formations (Cui et al. 2017). The Kootenai River basin is characterized by high variability in ^{87}Sr:^{86}Sr among the different tributaries, generally following the expected patterns based on the large heterogeneity of the underlying geologic formations (Dunnigan et al. 2023; Ghere et al. 2024).

2.2 | Fish Collection

In 2014, age-0 Redband Trout were collected from throughout the Kootenai River basin to use as known-origin ^{87}Sr:^{86}Sr references for the different stream reaches (Table 1, Figure 1). When possible, sampling was conducted at least 0.5 km upstream from the mouth of the tributary to minimize the occurrence of collecting fish that may have moved from other streams. The Fisher River, Yaak River, and Big Cherry Creek were sampled in two locations, both upstream and downstream of falls considered barriers to upstream fish passage. Age-0 Redband Trout were collected using a backpack electrofishing unit.

Redband Trout of unknown origin were collected by boat electrofishing in the mainstem of the Kootenai River during fall (i.e., August–November) of 2014–2015. Fish were collected by IDFG and the Montana Department of Fish, Wildlife, and Parks (MTFWP). Additional fish were collected by IDFG in 2023 by boat electrofishing. In Idaho, Kootenai River reaches approximately 1 km in length were sampled every 10 km from the Idaho-Montana border to the Idaho-British Columbia border with a goal of collecting five Redband Trout per 10 km (Figure 1; Rust et al. 2017). Sampling conducted by IDFG in 2023 occurred in 1 km long reaches at long-term monitoring sites (two in the braided reach, one in the canyon reach). Sampling conducted by MTFWP occurred in 2014 and 2015 at four long-term population monitoring sites 3–6 km in length (Rust et al. 2017). Otoliths were also opportunistically collected from Redband Trout harvested by anglers and mortalities observed in the Kootenai River. In both Idaho and Montana, fish were measured for total length (mm). Sagittal otoliths from all Redband Trout were removed and stored dry in coin envelopes until later processing.

2.3 | Water Sample Collection and Processing

Water samples were collected to corroborate natal ^{87}Sr:^{86}Sr values from known-origin Redband Trout. All water sampling collection equipment was acid washed, air dried, and then stored in Whirl Pak bags (Nasco, Fort Atkinson, WI) until use in the field (Shiller 2003). Water samples were collected with 10 mL syringes and filtered using 0.2 μm pore filters (GE, Pittsburgh, PA). Water samples (50 mL) were collected in 2015 from tributaries and the mainstem Kootenai River (Table 1). Additional samples were collected in 2023 from sites in the Kootenai River ranging from Troy, Montana, to the lower Goat River, British Columbia.

2.4 | ^{87}Sr:^{86}Sr Analysis

One sagittal otolith per fish was mounted sulcus acusticus side down on a microscope slide using thermoplastic cement (Crystalbond 509-3, Aremco, Valley Cottage, NY). Otoliths were sanded using a Buehler MetaServ 250 (Buhler, Lake Bluff, IL) grinder-polisher with 400–1200 grit sandpaper and ultrapure water until the distal side of the otolith was flat (Chase et al. 2015; Heckel et al. 2020). The otolith was flipped (i.e., sulcus acusticus side up) and sanded until the primordium and daily growth rings were clearly visible using a compound microscope. Otoliths were mounted on petrographic slides using thermoplastic cement and cleaned with ultrapure water (Barnett-Johnson et al. 2008).

Samples were taken to the Interdisciplinary Center for Plasma Mass Spectrometry at the University of California-Davis (UC Davis) for strontium isotope ($^{87}Sr:^{86}Sr$) analysis 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 proceeded from edge to edge, transecting the core at a beam width of 40–55 μm, scanning speed of 10 μm/s, and a laser pulse frequency of 20 Hz (see supplemental information; Table S1). Data reduction and analysis was completed using the IsoFishRscript (Willmes et al. 2018) in Program R (R Core Team 2024). Briefly, we normalized for mass bias ($^{86}Sr:^{88}Sr = 0.1194$), applied an ^{87}Rb interference correction, and an on-peak subtraction for ^{86}Kr. We then applied a 5-point average to the raw data collected by the mass spectrometer with an integration time of 0.2 s, resulting in one data point per second, and removed outliers based on a 20-point moving interquartile range (IQR) criterion. Profile data for each fish were created by smoothing the reduced data using a thin-plate regression spline ($k = 100$) and generalized cross-validation with the mgcv package in Program R (Wood 2017). At the beginning and end of each slide, instrumental accuracy was evaluated by measuring a White Seabass *Atractoscion nobilis* otolith, which showed average values of 0.70917 ± 0.0001 (mean ± SD, $n = 93$), similar to the global average $^{87}Sr:^{86}Sr$ value of modern seawater of 0.70918.

After microchemistry analysis, otoliths were viewed with a dissecting microscope using transmitted light, and a single reader aged all fish. Using Image-Pro Plus (Media Cybernetics Inc., Bethesda, Maryland) the reader measured the distance between annuli along the ablation line.

Water samples were taken to UC Davis for $^{87}Sr:^{86}Sr$ analysis. $^{87}Sr:^{86}Sr$ values for each water sample were obtained using a Nu Plasma HR (Nu032) MCICP mass spectrometer with a desolvating nebulizer inlet system after calibration following methods described in Willmes et al. (2016; Nu Instruments DNS-100; North Wales, United Kingdom).

2.5 | Location Discrimination Models

For known-origin age-0 Redband Trout, the natal region was defined as the 50–100 μm region of the $^{87}Sr:^{86}Sr$ profile near the edge of the otolith representing the most recent environmental conditions and avoiding any maternal contribution (Barnett-Johnson et al. 2005, 2008; Brennan et al. 2015). $^{87}Sr:^{86}Sr$ mean and standard deviation were calculated and used for subsequent analysis. Water $^{87}Sr:^{86}Sr$ values were compared to otolith natal $^{87}Sr:^{86}Sr$ for each stream using linear regression. Each instance of inconsistency between natal otolith and water data was investigated.

The caret package in Program R (Kuhn 2008; R Core Team 2024) was used to develop random forest classification models for natal origin assignment. Random forest is a machine learning method that has been used with both multi- and univariate data for classification analyses (Mercier et al. 2011; Willmes et al. 2021; Dunnigan et al. 2023). Two models were developed to account for the upstream barrier at Kootenai Falls. The first model (Basin-wide model) was trained with all known-origin Redband Trout natal values, and the second model (Restricted model) was trained with only known-origin Redband Trout collected upstream of Kootenai Falls. Natal values from known-origin Redband Trout were used to develop the random forest models by splitting the data into training (80%) and testing (20%) datasets. Training data were then sampled with replacement for a sample size of 15 fish per stream. In total, 500 trees were generated for each model (Willmes et al. 2021) and the model hyperparameters (minimum datapoints per node before splitting) were tuned using 10-fold cross-validation. Overall model performance was evaluated using the test data and a confusion matrix approach (see supplemental material; Tables S4 and S5). In addition, posterior probabilities were examined for each fish to evaluate the reliability of model predictions. Posterior probabilities describe the percentage of trees generated by each model that assigned a fish to the corresponding tributary.

2.6 | Life History Analysis

Maternal and natal regions of unknown-origin Redband Trout were defined by visually inspecting $^{87}Sr:^{86}Sr$ profiles and following a set of guidelines to select the appropriate region (Figure 2; Barnett-Johnson et al. 2007; Miller and Kent 2009; Willmes et al. 2021). Annuli measurements were added to $^{87}Sr:^{86}Sr$ profile plots for reference during selection. Maternal values were estimated by averaging the $^{87}Sr:^{86}Sr$ values at a 30–100 μm region of the transect surrounding the primordium of each sample (Volk et al. 2000; Bacon et al. 2004). Natal values were derived from a 50–100 μm region of the stable portion of the $^{87}Sr:^{86}Sr$ profile adjacent to the maternal value (Barnett-Johnson et al. 2005, 2008; Brennan et al. 2015). Maternal and natal values of unknown-origin Redband Trout were then used to predict stream of origin by one of the random forest models based on capture location. Redband Trout captured downstream of Kootenai Falls were assigned locations using the Basin-wide model, whereas Redband Trout captured upstream of Kootenai Falls were assigned using the Restricted model. The life history of each fish's mother was described as migratory if the maternal stream assignment differed from the natal stream assignment and resident if both maternal and natal stream assignments were the same. Furthermore, Redband Trout were described as migratory if an inflection on the $^{87}Sr:^{86}Sr$ profile was observed following the natal region and resident if the profile remained unchanged. Similar techniques have been used to estimate the life history characteristics of other fish species in multiple systems (Cook and Bourret 2022; Dunnigan et al. 2023; Goto et al. 2024). Adfluvial and fluvial life history types were indistinguishable

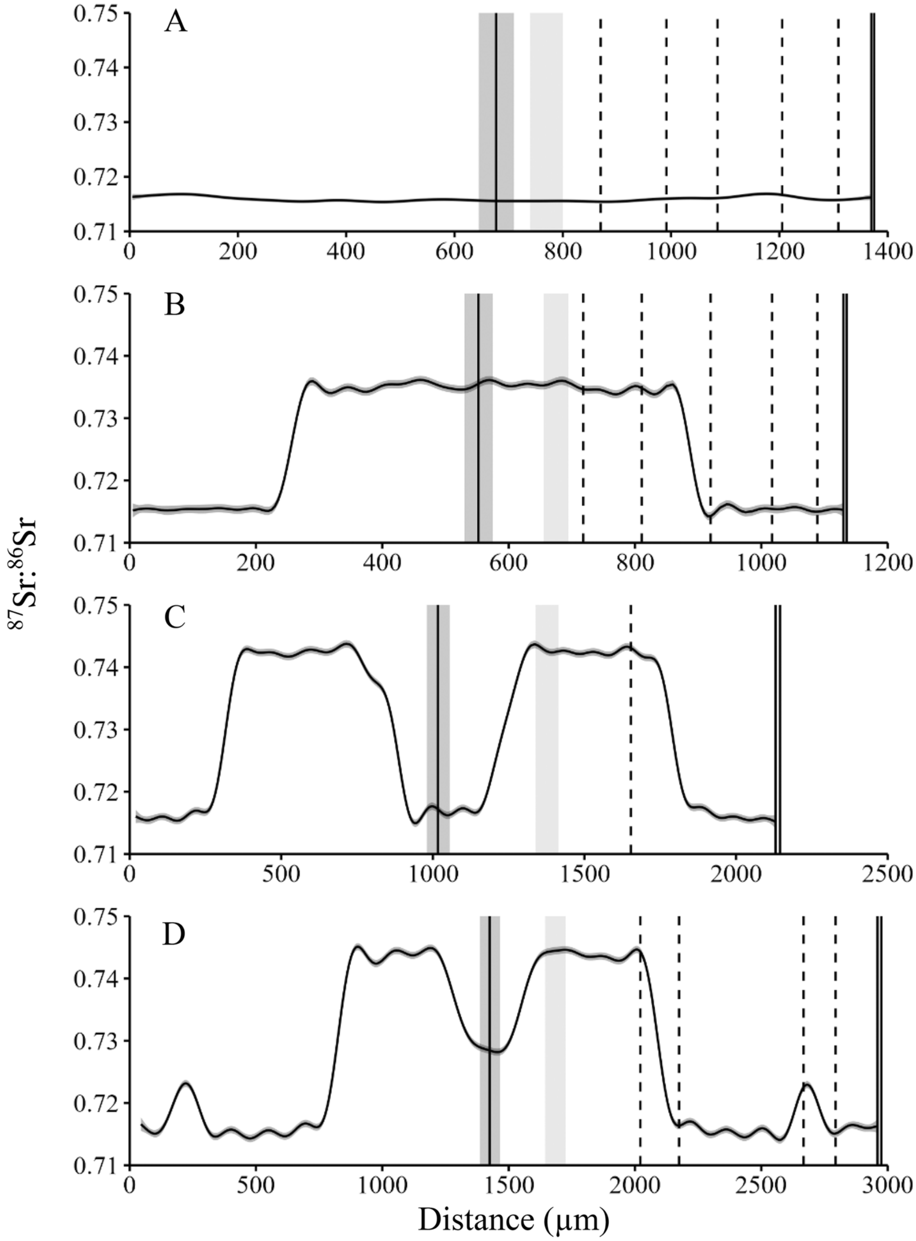

FIGURE 2 | Example ^{87}Sr:^{86}Sr profile plots from otolith ablation of Redband Trout with varying life history types including mainstem resident with mainstem resident mother (A), migrant with tributary resident mother (B), migrant with migrant mother (C), and migrant with migrant mother and potential tributary migration at age 3 (D). Redband Trout were sampled in the Kootenai River in 2015 and 2023. The x-axis runs from 0 µm at the ventraledge of the otolith to 2130 µm at the dorsaledge of the otolith. Gray shading along the profile line represents 2SE of ^{87}Sr:^{86}Sr values. The mean values of the shaded regions were calculated and used as maternal (dark gray bar) and natal values (light gray bar). Vertical lines mark the core (solid), annuli (dashed) and edge (double solid) measured during otolith ageing.

due to the inability of ^{87}Sr:^{86}Sr to differentiate between Kootenay Lake and the Kootenai River (Ghere et al. 2024).

Age and length at outmigration were estimated for each unknown-origin Redband Trout. Outmigration was defined as the point at which an inflection on the ^{87}Sr:^{86}Sr profile occurred following the natal region. Age at outmigration was the age preceding the outmigration inflection point. Length at outmigration was back calculated (Dahl-Lea; Francis 1990; Quist et al. 2012) using the distance between the core and inflection point. Migratory movements were defined as subsequent peak and valley inflections of ^{87}Sr:^{86}Sr profiles following outmigration. Differences in life history characteristics were evaluated at the habitat reach scale (i.e., meander, canyon). Distance moved from natal stream was estimated as the absolute distance (RKM) between the mouth of the assigned natal tributary and the location of capture in the mainstem Kootenai River. Redband Trout captured in the spring were excluded from estimates of migration distance in an effort to reduce potential bias from individuals making spawning migrations. Age and length at outmigration data and absolute distance moved were compared between habitat reaches using the Wilcoxon rank sum test as they did not meet parametric assumptions (Blair and Higgins 1980). A type-I error rate of $\alpha = 0.05$ was used for all statistical tests.

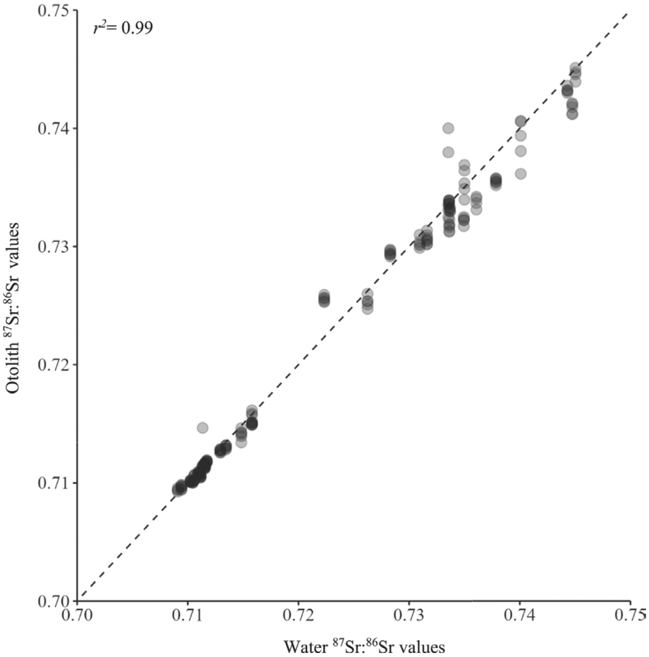

FIGURE 3 | Comparison of ^{87}Sr:^{86}Sr values from water samples to values obtained from age-0 Redband Trout otoliths collected in the Kootenai River and its tributaries. Water samples were collected in 2014 and 2022, and Redband Trout otoliths were collected in 2014. The dashed line represents a 1:1 ratio for reference. Darker shading indicates overlapping points.

3 | Results

3.1 | Water and Known-Origin Otolith ^{87}Sr:^{86}Sr Comparison

Known-origin otolith ^{87}Sr:^{86}Sr varied from 0.6993 to 0.7514, and values of ^{87}Sr:^{86}Sr in water samples varied from 0.7091 to 0.7461 throughout the Kootenai River basin (Table 1). Values of ^{87}Sr:^{86}Sr obtained from water and known-origin otolith samples were similar ($r^2 = 0.99$; Figure 3). In general, ^{87}Sr:^{86}Sr values were highest in tributaries in the canyon reach, followed by the Kootenai River and tributaries in the meander reach. The only exceptions were Mission Creek and Boundary Creek (both tributaries in the meander reach), which had values greater than those from the Kootenai River (Table 1; Figure 1). Inconsistencies between water and otolith data were identified in four tributaries (i.e., Burton Creek, Curley Creek, Fall Creek, Moyie River) and were attributed to recent movement of the age-0 fish from other tributaries. Consequently, these otolith data were omitted from further analyses.

3.2 | Location Discrimination Models

Age-0 Redband Trout ($n = 244$) from 35 streams and the Kootenai River were used to create the Basin-wide random forest model. Accuracy of the Basin-wide model using the testing dataset was 93.7% (CI = 90%–97%; kappa = 0.94). The Restricted model was developed using 75 age-0 Redband Trout from 13 tributaries and the mainstem Kootenai River upstream of Kootenai Falls. The Restricted model predicted known-origin Redband Trout to the 14 natal sites above Kootenai Falls with 98.1% accuracy using the testing dataset (CI = 91%–100%; kappa = 0.98). All errors in prediction assigned fish to tributaries within the same habitat reach (see supplemental material; Tables S4 and S5). For both models, the posterior probability of each fish being assigned to a given site was 59% or greater, with the majority of fish (89.9%) having posterior probabilities of 75% or greater. Given the large number of potential source sites, we decided to keep fish with relatively low posterior probabilities (< 75%) in the analyses but note that their natal assignments are more uncertain than the majority of the studied fish.

3.3 | Life History Analysis

Life history characteristics were described for 329 unknown-origin Redband Trout. Unknown-origin Redband Trout varied in length from 84 to 864 mm and from age 1–8. Approximately 18.5% of Redband Trout natal values were assigned to the mainstem Kootenai River. Redband Trout with mainstem natal assignments were most often captured at sites in the canyon reach of the Kootenai River with maternal values also assigned to the mainstem Kootenai River (87.5%).

The remaining Redband Trout were assigned natal origins in 31 of the 35 tributaries present in the random forest models (Figure 4). Tributaries with no natal assignments were all in the meander reach (i.e., Long Canyon, Parker, Ruby, and Snow creeks). Most migratory Redband Trout were assigned to tributaries in the canyon reach of the Kootenai River (88.1%) and had migratory maternal values (77.2%). Tributaries with the most Redband Trout natal-origin assignments were Flower Creek ($n = 45$) and Bobtail Creek ($n = 44$). In addition to using our random forest models to predict whether a mother was migratory or resident, we examined the percent difference in maternal and natal values (Figure 5). We found that the maternal values described as migratory ($n = 206$) had a difference from natal values that varied from 0.00006% to 2.8% with a mean of 1.2% difference, and all maternal values described as non-migratory ($n = 61$) had a difference that varied from 0.000003% to 0.005% with a mean of 0.1% difference between values.

Age at outmigration throughout the Kootenai River basin varied from 0 to 3 years. Although age of outmigration was not significantly different between reaches [Wilcoxon test statistic (W) = 3394, $p = 0.31$], a greater proportion of streams in the canyon reach were assigned Redband Trout that out-migrated at age 0 (Figure 6). Average estimated length at outmigration was 137 mm (SD = 68 mm) and varied from 12 to 430 mm. Length at outmigration was similar between reaches ($W = 2870$, $p = 0.21$).

Movement distances were estimated for Redband Trout captured from August to November ($n = 240$). Distances moved from assigned natal tributaries by Redband Trout varied from 0 (at the mouth of the tributary) to 153 km, with an average of 34.6 km (SD = 34.4 km; Figure 7). The absolute distance moved by fish originating in the meander and canyon reaches was similar ($W = 2459$, $p = 0.22$). The farthest estimated movement was a fish that originated in Bobtail Creek and was captured 153 km downstream in the Kootenai River near Boundary Creek. The farthest upstream movements were from three fish that originated in Mission Creek and ascended 76 km to capture near

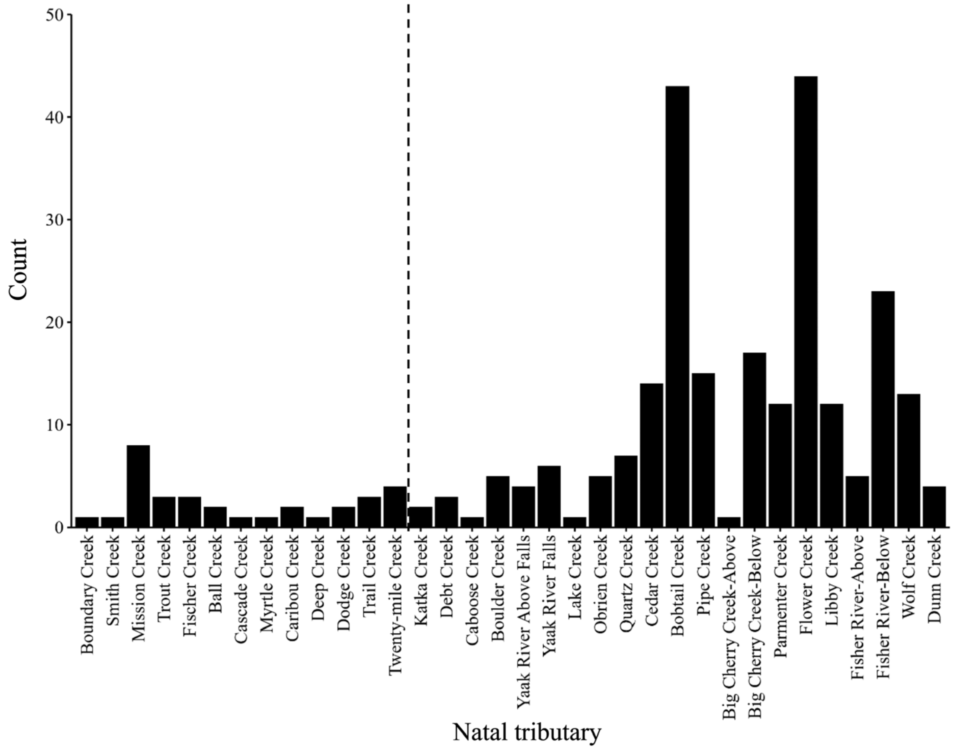

FIGURE 4 | Number of unknown-origin migratory Redband Trout assigned natal habitats in tributaries of the Kootenai River. Natal tributaries are listed from downstream to upstream, with Boundary Creek being the most downstream tributary and Dunn Creek the most upstream tributary. The vertical dashed line is the division between meander and canyon reach tributaries.

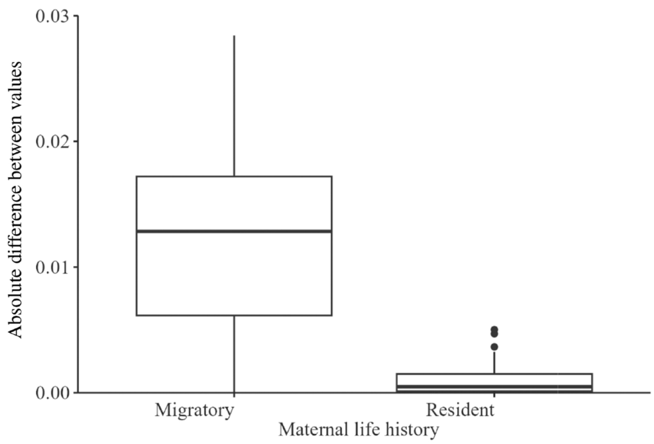

FIGURE 5 | Comparison of the absolute difference between maternal and natal values of Redband Trout sampled in the Kootenai River with maternal life histories described as migratory or resident.

the Idaho–Montana border. Canyon reach tributaries produced Redband Trout that most often moved downstream. Fish from the meander reach tributaries were most often captured upstream of their natal tributaries. A small number of Redband Trout sampled ($n = 13$) had post-outmigration movements between tributaries and the Kootenai River identified on their ^{87}Sr:^{86}Sr profiles.

4 | Discussion

Variable life history structure has been described in many salmonid populations, and Redband Trout may express several life history types (e.g., anadromous, fluvial, resident; Muhlfeld et al. 2015). Variation in life history characteristics of Redband Trout was observed throughout the Kootenai River basin. Despite limitations in the ability to distinguish fluvial from adfluvial life history types, we were able to identify general life history types (i.e., migratory, resident) and describe the relationship between life-history type of Redband Trout and their mothers in the Kootenai River. Redband Trout in the Kootenai River originated from both mainstem and tributary spawning areas and were documented moving large distances (> 150 km) throughout the basin.

Life history diversity may increase resiliency of fish populations by promoting genetic diversity and buffering the effects of environmental variability (Behnke 2002; Dodson et al. 2013; Moore et al. 2014). Redband Trout have been found to reproduce with individuals of differing life history types, producing offspring that express a variety of life history strategies (Pearsons et al. 2007; Currens et al. 2009; Holecek et al. 2012). For example, Dobos et al. (2020) described over a dozen life history forms of steelhead (i.e., anadromous Redband Trout) in one Idaho stream. The use of various rearing habitats may also reduce the influence of environmental effects on fluctuations in fish populations.

Redband Trout in the Kootenai River originated from natal habitats throughout the Kootenai River basin. Mainstem spawning contributed an unexpected number of Redband Trout. Nearly 20% of Redband Trout sampled in the Kootenai River were assigned natal origins in the mainstem river. To our knowledge, mainstem spawning has not previously been reported in the Kootenai River basin. Walters (2001, 2002, 2003, 2004) evaluated the movement of Rainbow Trout (used interchangeably with Redband Trout in the Kootenai River)

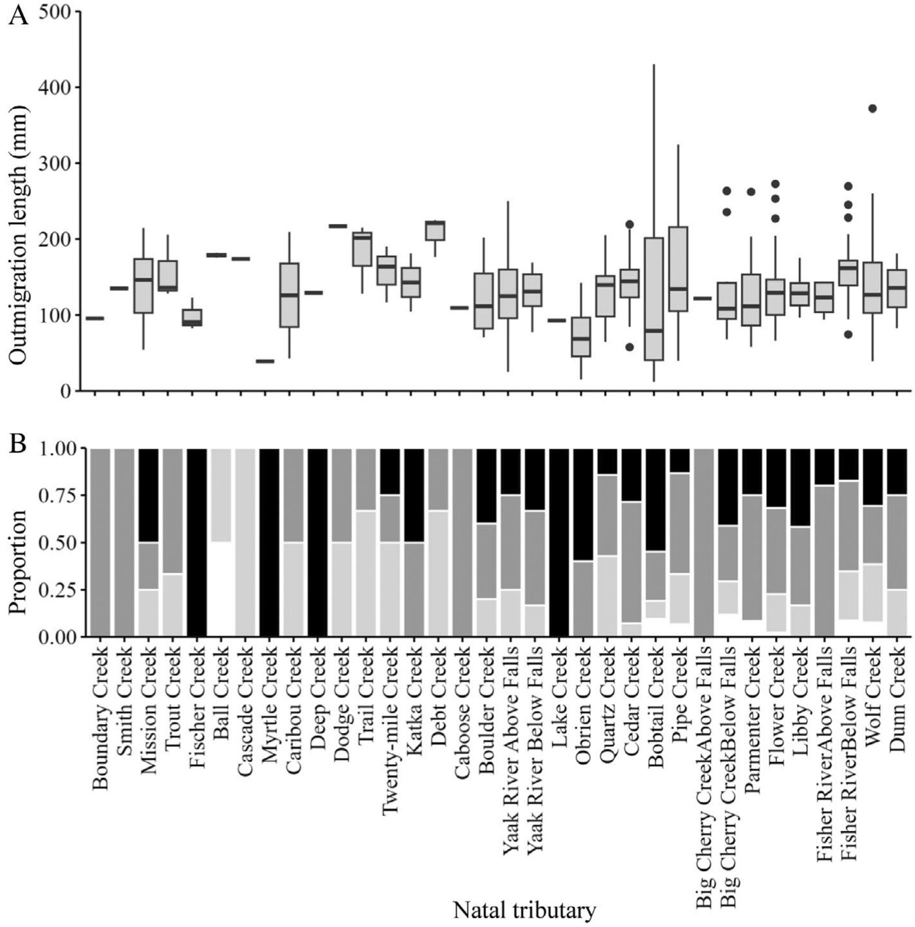

FIGURE 6 | Outmigration characteristics of Redband Trout sampled in the Kootenai River in 2014, 2015, and 2022. Natal tributaries are listed from downstream to upstream, with Boundary Creek being the most downstream tributary and Dunn Creek the most upstream tributary. (A) is the proportion of Redband Trout that out-migrated at each age from Kootenai River tributaries. (B) is the length at outmigration of Redband Trout originating in each natal tributary (black = age 0, dark gray = age 1, light gray = age 2, white = age 3).

in the Kootenai River basin using radio telemetry and detected no mainstem spawning activity. Mainstem spawning of Rainbow Trout has been observed in other populations. Salmonid spawning activity was monitored using radio transmitters in the South Fork Snake River, Idaho, and most of the Rainbow Trout observed spawned in mainstem habitat (Henderson et al. 2000). DeRito et al. (2010) reported mainstem spawning of Rainbow Trout in the Yellowstone River, Montana, though at a lower rate than observed by Henderson et al. (2000). Despite a lack of observed mainstem spawning, the results of Walters (2001, 2002, 2003, 2004) were consistent with our research in suggesting that tributaries in the canyon reach are important sources of Redband Trout in the Kootenai River.

Tributaries in the meander reach of the Kootenai River were the source of substantially less Redband Trout (< 12%) sampled in this research than tributaries in the canyon reach. Previous research suggests that the Rainbow Trout distribution is influenced by large-scale habitat characteristics. Muhlfeld et al. (2001a) described the summer habitat use of Redband Trout in two tributaries of the Kootenai River (i.e., Basin and Callahan creeks). Redband Trout were most commonly observed in low gradient streams (< 5%) with low velocity and deep pools. Meyer et al. (2014) sampled Redband Trout in over 1000 stream reaches throughout the upper Snake River basin, Idaho. Like Muhlfeld et al. (2001a), the authors found that Redband Trout were most common in mid-sized, low gradient streams. In the Kootenai River system, large-scale habitat characteristics (i.e., discharge, gradient, temperature) of tributaries in the meander and canyon reaches are quite similar. For example, the estimated mean August temperature is 12.4°C (SE = 0.3) for tributaries in the canyon reach and 11.9°C (SE = 0.4) for tributaries in the meander reach (Isaak et al. 2017). Excluding very large tributaries (i.e., Yaak River, Fisher River), mean historic August discharge is also similar between the canyon reach (0.48 cms, SE = 0.16) and meander reach (0.35 cms, SE = 0.08; Wenger et al. 2010). Similarities in large-scale habitat characteristics throughout the Kootenai River basin indicate that differences in the quantity of Redband Trout originating from tributaries are most likely related to differences in fine-scale habitat characteristics.

Previous research has identified associations between juvenile Rainbow Trout abundance and fine-scale habitat characteristics. Muhlfeld et al. (2001b) described the fall and winter habitat use of Redband Trout in Callahan Creek, a tributary of the Kootenai River. Redband Trout were most abundant in stream reaches that contained deep pools and large substrate with

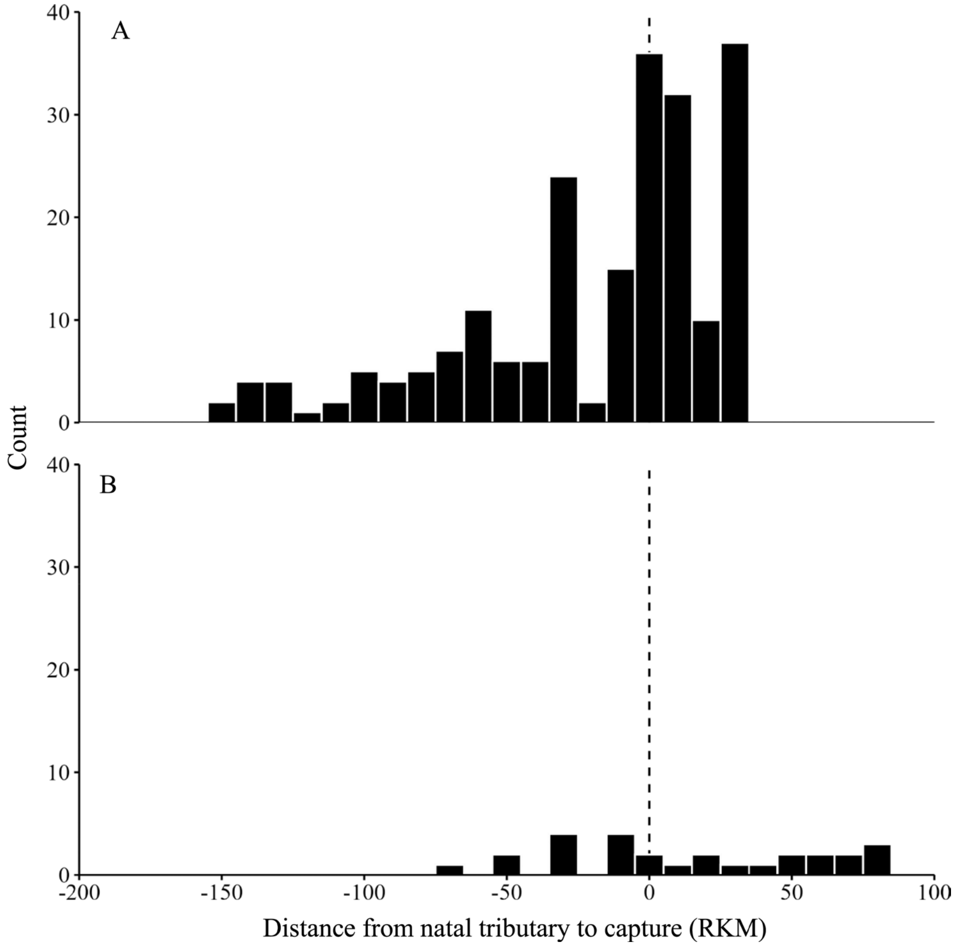

FIGURE 7 | Distance in river kilometers (RKM) between natal tributary mouth and capture location of Redband Trout in the Kootenai River sampled during the months of August to November in 2014 and 2015. (A) Contains Redband Trout that originated from canyon reach tributaries; (B) contains fish that originated in meander reach tributaries. The dashed line at zero indicates capture near the confluence of the assigned natal tributary and the Kootenai River; negative observations represent downstream movement, and positive observations represent upstream movement.

interstitial spaces for cover. Similarly, in Rock Creek, California, Baltz et al. (1991) found that juvenile Rainbow Trout abundance was greatest in areas with deep, low-velocity pools and large substrate. Culp et al. (1996) conducted an experiment in Jumping Pound Creek, Alberta, to assess the influence of woody debris on juvenile Rainbow Trout abundance. The authors found that woody debris increased the quality of rearing habitat by providing protection from predation. Meyer and Griffith (1997) conducted enclosure experiments in the Henry's Fork of the Snake River, Idaho, to evaluate the influence of substrate type on the movement of juvenile Rainbow Trout. Rainbow Trout remained in habitats with substrate that provided cover regardless of fish density, demonstrating the influence of habitat on juvenile fish movements. Few surveys have been conducted that evaluate fine-scale habitat characteristics in tributaries of the Kootenai River basin. Therefore, it is unknown whether fine-scale habitat is a major factor limiting Redband Trout recruitment in the lower Kootenai River basin. However, there are known differences in land use of the areas surrounding the meander and canyon reaches. Specifically, almost all tributaries of the meander reach pass through agricultural land, compared to little agricultural land in the watersheds of tributaries in the canyon reach (KTOI 2009). Streams in agricultural areas typically experience high sediment input, degraded streambanks, embedded substrates, and little channel complexity (Walser and Bart Jr. 1999; Gilliom 2007). Further investigation of fine-scale habitat characteristics throughout the Kootenai River basin could potentially identify opportunities to improve the quality and quantity of rearing habitat for juvenile Redband Trout in tributaries of the meander reach.

Tributaries in the meander reach of the Kootenai River have seemingly retained life history diversity despite habitat degradation and disconnection. Although tributaries in the meander reach contributed far fewer Redband Trout to sampling in this study than tributaries in the canyon, 76.5% of tributaries sampled in the meander reach were a source of Redband Trout. Based on historical sampling, Deep Creek was expected to contribute the greatest number of Redband Trout in the meander reach (Walters 2005). Although Deep Creek itself did not have many Redband Trout assignments in our study, the Deep Creek subbasin (i.e., Caribou, Dodge, Trail, Twenty-mile creeks) contributed a substantial proportion of the Redband Trout that originated from the meander reach (37.5%). However, three of the four streams that lacked natal Redband Trout assignments also occurred in the Deep Creek watershed. Further investigation of Redband Trout recruitment in tributaries of the Deep Creek watershed would likely provide a more thorough understanding of the importance of the system to the Redband Trout population. Another tributary in the meander reach, Mission Creek, has over 3 km of leveed, straightened channel in the lower reach of the stream and a barrier to fish passage at 4.2 km. Despite a degraded migratory corridor and the relative rarity of Redband Trout in the system (Walters 2007), Mission Creek contributed the greatest number of Redband Trout in the meander reach. Another unexpected source of Redband Trout in the Kootenai River was several streams that contained apparent barriers to fish passage. Paragamian (2008) evaluated barriers to fish passage in Idaho tributaries of the Kootenai River. Caboose, Debt, and Twenty-mile creeks were found to have quality spawning habitat separated from the Kootenai River by perched culverts thought to act as barriers to fish movement. All three streams contributed Redband Trout sampled in this research, suggesting that Redband Trout contributions from these streams may be increased by improving passage to spawning habitat. Confirming the contributions of degraded and disconnected natal tributaries to the Kootenai River Redband Trout population provides a starting place for investigating Redband Trout conservation options into the future. The life history type of Redband Trout typically reflected their mother's, but some resident mothers produced migratory offspring. Maternal values may incorrectly be assigned as resident in cases where an early migrating mother develops eggs in a natal tributary instead of the mainstem river. However, based on observations of the timing of Redband Trout spawning migrations in the Kootenai River basin, such instances are likely rare in this study system (Muhlfeld 2002; Walters 2004). Alternatively, maternal values can also be incorrectly assigned as migratory if seasonal or within-river variability exceeded what we predicted based on the random forest classification models. Even considering these uncertainties in the designations of maternal phenotypes, our observations still show that there is likely connectivity between resident and migrant phenotypes.

Age and length at outmigration varied throughout the Kootenai River basin. Although mean age at outmigration was not significantly different between the canyon and meander reaches, more tributaries in the canyon reach were a source of Redband Trout that outmigrated at age 0. The observed variation in outmigration age and length throughout the basin provides further evidence of substantial life history diversity at both the watershed and tributary scales. Variation in outmigration timing of Redband Trout in the Kootenai River basin is consistent with the variability observed in other salmonid populations. A variety of biotic (e.g., density, productivity) and abiotic (e.g., temperature, substrate) factors influence outmigration timing in salmonids (Bjornn and Reiser 1991). For example, Dobos et al. (2020) monitored the outmigration of steelhead from Fish Creek, Idaho, over multiple decades and found that outmigration timing was related to biotic factors. Specifically, years with high juvenile density and younger outmigration ages followed high numbers of returning adult females. Abiotic and biotic factors may also interact to influence outmigration timing. Ohms et al. (2014) studied Rainbow Trout from nine streams across the western United States and found that sex was the best predictor of life history type (i.e., anadromous or resident) and that outmigration age decreased with latitude (i.e., increased growth opportunity). In a study of Bull Trout *Salvelinus confluentus* outmigration in Graves Creek, Montana, Lewis et al. (2022) described the influence of biotic and environmental factors. The total number of outmigrating fish changed over time in relation to changes in discharge, photoperiod, water temperature, and relative size. As described for other salmonids, the diversity of Redband Trout outmigration and life history characteristics has likely led to population resiliency in the Kootenai River basin (Schindler et al. 2010; Haak and Williams 2012).

The identification of natal tributaries and life history characteristics of Redband Trout in the Kootenai River has contributed to the development of conservation planning in the Kootenai River basin. However, life history information is not the only factor to consider when planning and evaluating conservation efforts. The habitat requirements of fishes are complex and change with life history stage (Bjornn and Reiser 1991; Rosenfeld 2003). Prioritization of restoration activities also requires the integration of factors, including genetics (Vrijenhoek 1998; Epifanio et al. 2003; Allendorf 2017), pre-existing habitat characteristics (Roni et al. 2018), and economic feasibility (Meehan 1991; Null and Lund 2012). Tributaries in the canyon reach currently contribute the majority of Redband Trout to the basin, and protection of natal habitat in those streams would help to maintain important Redband Trout habitat. Tributaries in the meander reach contribute far fewer Redband Trout to the Kootenai River than tributaries in the canyon reach. However, the meander reach has the potential for increased recruitment due to the retention of life history diversity. Improved fish passage in tributaries could further increase recruitment of Redband Trout in Idaho. Understanding Redband Trout population dynamics in the Kootenai River basin could also be improved by identifying differences in fluvial and adfluvial Redband Trout and by investigating the prevalence of tributary residents. Nearly 30% of the migratory fish sampled in this study had tributary resident maternal values, demonstrating the importance of resident life history to the Redband Trout population in the Kootenai River. The results of this research provide another source of information for managers prioritizing conservation efforts and planning evaluation methods for Redband Trout in the Kootenai River basin. Overall, our research contributes to knowledge about Redband Trout life history characteristics and the insights that microchemistry analysis can provide when prioritizing conservation efforts for native species.

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Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Instrument operating conditions of the Nu Plasma HR (Nu032) and New Wave Research UP213 Nd:YAG 213 nm laser. **Table S2:** Minimum, maximum, mean, and standard deviation (SD) of posterior probabilities from the basin-wide random forest model for Redband Trout in the Kootenai River system. A stream identification (ID) code is provided for other supplemental tables. **Table S3:** Minimum, maximum, mean, and standard deviation (SD) of posterior probabilities from the restricted random forest model for Redband Trout in the Kootenai River system. A stream identification (ID) code is provided for other supplemental tables. **Table S4:** Confusion matrix based on predictions from the basin-wide random forest model for Redband Trout in the Kootenai River system. Stream identification is provided in the first row and column (see Table S1). Actual location is provided in the first row and predicted location is provided in the first column. Correct classifications are shown in light gray and errors are highlighted in dark gray. **Table S5:** Confusion matrix based on predictions from the restricted random forest model for Redband Trout in the Kootenai River system. Stream identification is provided in the first row and column (see Table S1). Actual location is provided in the first row and predicted location is provided in the first column. Correct classifications are shown in light gray.