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Otolith $^{87}Sr/^{86}Sr$ identifies natal origin, movement and life history of Burbot *Lota lota* in the Kootenai River following 45 years of impoundment

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Abstract

Hydropower has long been an effective form of renewable energy, but the development of the resource has negatively impacted fishes throughout the world. Formulating recovery plans to mitigate these effects requires a firm understanding of species-specific provenance, life history and life stage habitat requirements. However, the importance of this information is often only recognised after a substantial population decline, when obtaining it becomes demographically challenging. We provide a case study for this scenario and present a post hoc approach to gain insight into these critical data gaps for Burbot *Lota lota* in the upper Kootenai River in Montana and British Columbia. The population once supported a robust tribal and recreational harvest but declined following impoundment and these fisheries have remained closed or curtailed for nearly 20 years. The reasons for the decline are unknown and actions to assist recovery have been constrained by limited information regarding natal origin, life history and habitat use. We addressed this issue using strontium isotope ratios ($^{87}Sr/^{86}Sr$) in otoliths collected over four decades in Lake Koocanusa, the reservoir on the Kootenai River above Libby Dam. Due to the geologic heterogeneity of the basin and resulting variation in water $^{87}Sr/^{86}Sr$, the assignment probability for Burbot to their region of natal origin approached unity. Otolith $^{87}Sr/^{86}Sr$ also indicated the population was comprised of mainstem- and tributary-origin forms and their relative abundance changed over time. Mainstem Burbot was most abundant during the 1970s and 2000s, whereas tributary forms dominated between these periods. We suggest ecosystem changes following impoundment contributed to this shift in life history forms and the overall decline of the population. Our findings underscore the need for additional investigations of these impacts to guide restoration efforts.

KEYWORDS

Burbot, ear stone, impoundment, natal origin, otolith, population decline, strontium isotope

1 | INTRODUCTION

Hydropower systems offer substantial benefits in the form of renewable energy, consumptive water, flood control and recreation, but the construction and operation of the dams that produce these benefits can impose adverse effects on aquatic habitats and hydrologic cycles of freshwater ecosystems (Harrison et al., 2016; Rosenberg et al., 1997). These effects can be expressed in both upstream and downstream environments (Harrison et al., 2016), and their direction and magnitude are often site-specific, depending on the purpose and operation of the structure. For example, dams that provide large reservoir storage capacity to reduce downstream flood risk and generate electricity often retain water during high flows and later release it during periods that would not typically experience high discharge. These operations can cause substantial daily and seasonal variation in downstream flow (Elliott & Hammack, 2000; Poff et al., 1997), temperature (Lessard & Hayes, 2003; Saltveit et al., 1994), water chemistry (Baxter, 1977), sedimentation (Dauble et al., 2003) and nutrient delivery (Hu et al., 2012; Woods, 1982) and alter habitats in ways that favour non-native fishes (Brown & Ford, 2002; Murphy et al., 2021). Many fish species have also evolved life history strategies to coincide with natural flow regimes (Lytle & Poff, 2004) that when altered by dam operations can lead to changes in residence (Hegg et al., 2019) and migration timing (Smith et al., 2003) and negatively impact spawning, incubation and early rearing areas (Dauble et al., 2003). Winter water level fluctuations in reservoirs, for instance, can reduce reproductive success through dewatering or by limiting access to littoral or tributary spawning grounds (Gaboury & Patalas, 1984; Wilcox & Meeker, 1992). Moreover, for winter spawning species such as Burbot *Lota lota*, thermal stress from the discharge of warmer hypolimnetic water during early embryonic development can potentially reduce larval recruitment due to increased deformity and mortality at hatch (Ashton et al., 2021).

In contrast to downstream environments, the ecological impacts of reservoir operations upstream of dams on fishes more often result from indirect effects beginning at lower trophic levels that influence population productivity and overall biomass (Carmignani & Roy, 2017; Hirsch et al., 2017). Reservoir operations that change water turbidity, oxygen and temperature (Gebre et al., 2014) or the availability and cycling of nutrients (Cooke, 1980) can influence the abundance and composition of phytoplankton (Baxter, 1977) and the macrophyte communities that provide important habitat for fishes (Wilcox & Meeker, 1992) and macroinvertebrates (Brown et al., 1988). These impacts can be exacerbated by water level fluctuations that alter the density, biomass and species composition of organisms in littoral and pelagic food webs, which in turn change the competition and predation relationships among and between fish species (Haxton & Findlay, 2008; Hirsch et al., 2017).

Burbot, the only freshwater member of the cod family *Gadidae*, exhibit life history variation across their circumpolar range (Scott & Crossman, 1998) that makes them particularly vulnerable to environmental perturbation from hydropower operations. They are found in lotic and lentic habitats, can be long-lived (15–20 years), highly fecund (>3 million eggs) and grow to large sizes (25–30 kg) (McPhail & Paragamian, 2000). Although comparatively poor swimmers (Jones et al., 1974; Paragamian et al., 2005), Burbot have been shown to make extensive (>200 km) and prolonged migrations (4–5 months) to littoral spawning sites with high synchrony and site fidelity (Jude et al., 2013; McPhail & Paragamian, 2000; Paragamian & Wakkinen, 2008), resulting in genetically distinct populations at varying geographic scales (Blumstein et al., 2018; Wetjen et al., 2020). Burbot also have highly specific thermal requirements for reproduction and embryonic development (Ashton et al., 2019; Harrison et al., 2016). Successful spawning and egg survival occur during the late winter and are closely linked to temperatures less than 4°C (Ashton et al., 2021). Impoundments that alter this thermal profile, impair spawning migration or dewater littoral spawning habitat and thus have the potential to negatively influence reproductive success and larval recruitment (Paragamian et al., 2005; Stapanian et al., 2010). Moreover, the high fecundity of Burbot produces a trade-off with egg size. Burbot produce small eggs (~1 mm diameter) that provide limited energy reserves prior to exogenous feeding (McPhail & Paragamian, 2000) and early survival is highly dependent upon suitable prey availability and size to match larval gape (Ghan & Sprules, 1993). Rotifers (Ghan & Sprules, 1993) and small copepods (Wang & Appenzeller, 1998) are important prey items at this time and hydropower operations that influence the spatial or temporal dynamics of these communities can limit food availability for the planktivorous larvae (Hardy & Paragamian, 2013).

Burbot are indigenous to the Kootenai River (Kootenay in Canada), a large (50,000 km^2) international watershed that encompasses portions of British Columbia (Canada), Montana and Idaho (United States). Genetic structuring of the species occurs within the watershed (Powell et al., 2008) that once supported robust tribal, recreational and commercial fisheries (Hardy & Paragamian, 2013; Paragamian et al., 2000). Estimates of total annual harvest during the 1960s exceeded thousands of kilograms (Paragamian et al., 2000). However, beginning in the early 1970s, the population downstream of Kootenai Falls (river kilometre [rkm] 311) began to decrease rapidly, and by 1983, the fisheries were curtailed and eventually closed (Paragamian et al., 2000). Coincident with this decline was the construction and operation of Libby Dam (rkm 357) in 1972 on the Kootenai River in Montana, although its effect on Burbot productivity in the watershed remains unclear. Unlike Burbot downstream of Libby Dam, the upstream population did not decline immediately after dam construction (Dunnigan et al., 2021). Relative abundance in Lake Koocanusa, the reservoir above Libby Dam, peaked in 1988, then slowly fell, especially over the past two decades. Low spawning success and early life stage survival appear to have contributed to this decline (Cope, 2019), but confirmation of this hypothesis has been hindered by limited knowledge of the natal origins, life history, spawning distribution and movement patterns of the Burbot populations upstream of Libby Dam. Radio tagging of Burbot in Lake Koocanusa over two spawning seasons by Dunnigan and Sinclair (2008) showed no evidence of movement upstream in the reservoir indicative of spawning migration, suggesting the Burbot inhabiting Lake Koocanusa was dominantly a lacustrine form.

Developing recovery plans for species of conservation concern requires an understanding of provenance, life history and life stage-specific habitat requirements (Griffith et al., 1989; Henry & Schultz, 2013). However, obtaining such information for the upper Kootenai River Burbot has been made difficult because of low abundance and an international boundary that has hindered permitting and field sampling. We addressed these constraints by examining strontium isotope ratios ($^{87}Sr/^{86}Sr$) in archival samples of Burbot otoliths collected over four decades. Strontium isotope ratios recorded in otoliths have been used to determine natal origin and reconstruct environmental history in many fishes (Brennan et al., 2015; Hegg et al., 2013; Walther & Limburg, 2012), including Burbot (Hooley-Underwood et al., 2018). Otolith $^{87}Sr/^{86}Sr$ typically exhibits a high correlation with water $^{87}Sr/^{86}Sr$ and can be an informative indicator of habitat use when there is heterogeneity in the age and type of geologic formations within and among watersheds (Brennan et al., 2014; Brennan & Schindler, 2017). The objectives of this study were to use otolith $^{87}Sr/^{86}Sr$ in archived samples to identify the natal origins of Burbot in Lake Koocanusa and examine their historic patterns of habitat use and movement. The goal was to provide resource managers with information to construct hypotheses related to the decline of this population and guide mitigation efforts should these be initiated to aid recovery.

2 | METHODS

2.1 | Study area

The upper Kootenai River watershed above Libby Dam can be broadly characterised by the geologic formations to the east and west of the river mainstem (Figure 1). Tributaries to the east originate and drain primarily from sedimentary rocks largely of the Palaeozoic era (~570 to 245 Ma), with younger sedimentary rocks of Mesozoic age (~250 to 65 Ma) present at higher elevations (Garrity & Soller, 2005). Sample sites located in these formations are hereafter referred to as Palaeozoic region sites. By contrast, tributaries entering the Kootenai River from the west flow through sedimentary formations that are dominant of the Middle Proterozoic era (~1500 Ma), with minor inclusions of intrusive rocks (e.g. igneous) from the Cretaceous period (~145 to 65 Ma) in the northern part of the formation. A narrow belt of Proterozoic rock also separates the mainstem from the Palaeozoic formation to the east and several small streams (e.g. Norbury Creek) drain from this area as well. Tributaries originating within and flowing primarily through this formation are hereafter referred to as Proterozoic region sites. We classified sites in the Kootenai River as the mainstem region and designated Canal Flats (Figure 1; No. 6 on the map) as the boundary between the mainstem and sites upriver from this point because the latter originate and flow entirely through Palaeozoic era rock.

2.2 | Sample collection

Water samples (1 per site) were collected by personnel from Montana Fish, Wildlife and Parks (MFWP) in August 2018 from 36 Lake Koocanusa and tributary sites (Table 1). The sample sites were chosen to obtain a broad-scale, spatial representation of water $^{87}Sr/^{86}Sr$ throughout the upper Kootenai River watershed. We focused on characterising spatial rather than temporal variation in water $^{87}Sr/^{86}Sr$ because studies have generally shown that in river basins with high geologic heterogeneity such as the upper Kootenai River, differences among streams tend to be greater than the seasonal and inter-annual differences within (Barnett-Johnson et al., 2008; Brennan et al., 2015; Hegg et al., 2013; Voss et al., 2014), although see Crook et al. (2016) for exceptions in tropical rivers. At the same time, a total of 142 fish (4–5 per site) were collected consisting of Columbia Slimy Sculpin *Cottus cognatus* (Richardson, 1836), Rainbow Trout *Oncorhynchus mykiss* (Walbaum 1792), Westslope Cutthroat Trout *O. clarkii lewisi* (Richardson, 1836), Redside Shiner *Richardsonius balteatus* (Richardson, 1836) and, Bull Trout *Salvelinus confluentus* (Suckley, 1859), (hereafter denoted as surrogate species) to establish stream-specific baseline values for otolith $^{87}Sr/^{86}Sr$. We prioritised collection of Columbia Slimy Sculpin because Sculpin have been shown to be non-migratory with limited home range (Brennan et al., 2015; Gray et al., 2018). When Sculpin were unavailable, we directed our collection efforts at Redside Shiner and young-of-the-year Rainbow, Westslope Cutthroat or Bull Trout to reduce the likelihood of sampling fish that may have moved from their natal stream. Archived samples of otoliths ($n = 147$) collected from Burbot captured during annual fisheries assessments were used to identify life history forms historically present in Lake Koocanusa and the contributions from mainstem and tributary habitats to the reservoir population. The Burbot were caught using gill nets and hoop traps between 1980 and 2016 (Dunnigan et al., 2021) and otoliths were selected that best represented annual collections within each decade (~40 per decade). However, samples were not available for each year nor were the sample sizes evenly distributed among years.

Water samples were collected in acid-washed (2% HNO_3) 60 mL perfluoroalkoxy (PFA) bottles following the procedures described by Linley et al. (2016). After shipment to the Pacific Northwest National Laboratory, the samples were filtered through PFA (1–2 μm) membranes, dried over low heat, and alternately treated with ultra-high purity 15 M nitric acid and 30% hydrogen peroxide to dissolve organic matter. After re-suspension in 7 M nitric acid, the samples were loaded onto Sr Spec cation exchange columns, washed again with 7 M nitric acid, and eluted with 0.05 M nitric acid to capture the available Sr. All sample preparation and column chemistry procedures were performed in a class 1000 clean lab, under a class 100 laminar flow hood.

Otoliths collected from surrogate fish species and archived Burbot samples were cleaned of residual endolymph and adhering

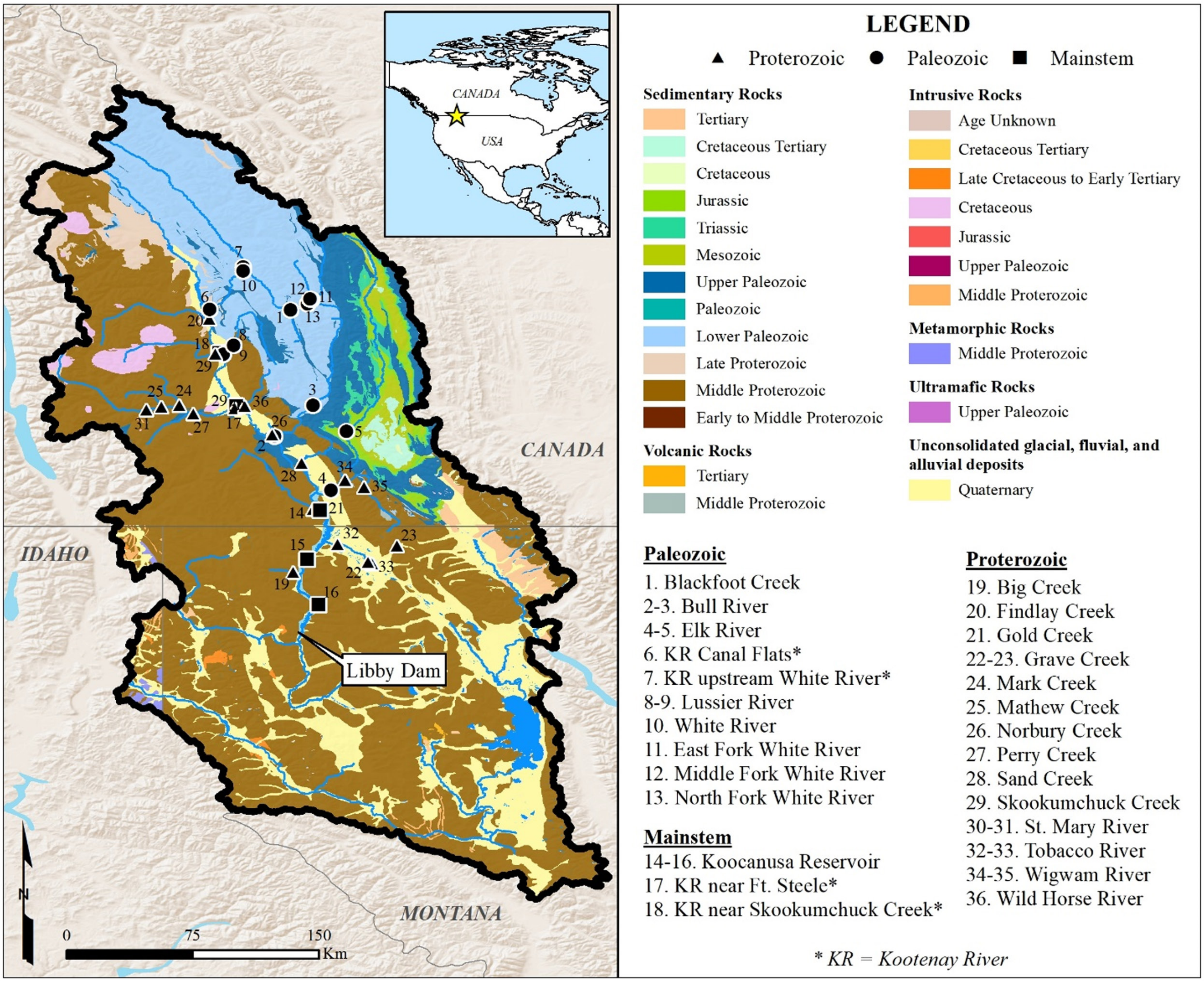

FIGURE 1 Map of the upper Kootenai River watershed indicating rock type, geologic era and sample sites (black symbols). Data from U.S. Geological Survey (https://mrdata.usgs.gov/geology/state/) and British Columbia Geological Survey (https://www2.gov.bc.ca/gov/content/industry/mineral-exploration-mining/british-columbia-geological-survey/geology/bcdigitalgeology).

tissue with DI water and then dried under a laminar hood until analysis. Burbot otoliths were embedded in a two-part epoxy and sectioned with a diamond blade wet saw (Buehler) to achieve ~1 mm sections prior to polishing. They were then prepared for analysis by attaching them to glass slides with thermoplastic glue (Crystal Bond 509) and polished with successively finer grit silicon carbide paper to produce thinner sections revealing the otolith core. Otoliths from surrogate fish species were also mounted on glass slides but in the sagittal plane and similarly polished with silicon carbide paper until the core was visible.

Otoliths were analysed for $^{87}Sr/^{86}Sr$ by laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) on a multi-collector ICP-MS Nu Plasma III (Nu Instruments) coupled to an NWR 213 nm Nd:YAg Laser (Electro Scientific Industries, Inc.). Before data collection, a cleaning pass of the otolith was performed with a laser beam size of 100 μm and power output of 10% to reduce potential contamination. The otoliths were ablated from core to edge, perpendicular to the sulcus with a beam width of 40 μm, 80% power, 10 Hz and a scan speed of 6 μm/s. On-peak zeroes were measured and subtracted prior to every run to remove the ^{84}Kr signal interference with ^{84}Sr, while a logarithmic correction of the measured $^{86}Sr/^{88}Sr$ to 0.1194 was applied to account for instrument mass fractionation. Marine coral standards were analysed at the beginning and end of each run (15–20 samples per run), and after 7–10 samples within runs to ensure that instrument tuning had not drifted, and that the $^{87}Sr/^{86}Sr$ value of modern seawater ($^{87}Sr/^{86}Sr = 0.70918$) was obtained within two standard errors (mean $^{87}Sr/^{86}Sr = 0.70918$, SE = 0.000003, $n = 35$). Washout times between measurements were approximately 1 minute, with the Faraday cup detector signals monitored to ensure a complete return to baseline values before subsequent runs. Water samples for $^{87}Sr/^{86}Sr$ were similarly analysed by multi-collector ICP-MS. Instrument performance was monitored by repeat analysis of SRM 987 yielding a mean value of 0.71023 ± 0.00003

TABLE 1 Water and surrogate fish otolith $^{87}Sr/^{86}Sr$ for Kootenai River mainstem and tributary streams in adjoining geologic formations.

Region	Site	Species	$^{87}Sr/^{86}Sr$ Water	Otolith	N
Palaeozoic	Blackfoot Creek	BLT	0.71074	0.71179 (0.00059)	4
	Bull River	SCU	0.71153	0.71130 (0.00008)	5
	Elk River	SCU	0.71079	0.71030 (0.00065)	5
	Kootenay River Canal Flats	SCU	0.71195	0.71220 (0.00077)	5
	Kootenay River Upper	SCU	0.71255	0.71254 (0.00042)	5
	Lussier River	SCU	0.71087	0.71111 (0.00029)	4
	White River	SCU	0.71171	0.71275 (0.00035)	5
	White River East Fork	SCU	0.71205	0.71219 (0.00060)	5
	White River Middle Fork	SCU	0.70889	0.70898 (0.00025)	4
	White River North Fork	SCU	0.71353	0.71265 (0.00063)	5
	Region Mean[a]		0.71146	0.71165 (0.00019)	47
	SD		0.00120		
Mainstem	Koocanusa Reservoir Rocky	RSS	0.71538	0.71523 (0.00028)	5
	Koocanusa Reservoir Yarrell	RSS	0.71517	0.71542 (0.00024)	5
	Koocanusa Reservoir Young Cr.	RSS	0.71426	0.71501 (0.00028)	5
	Kootenay River Ft. Steele	SCU	0.71573	0.71523 (0.00028)	5
	Kootenay River Skookumchuck Cr.	SCU	0.71463	0.71449 (0.00014)	5
	Region Mean[b]		0.71503	0.71573 (0.00058)	25
	SD		0.00059		
Proterozoic	Big Creek	SCU	0.74183	0.74133 (0.00011)	5
	Findlay Creek	SCU	0.73972	0.74337 (0.00071)	4
	Gold Creek	SCU	0.71955	0.71971 (0.00027)	4
	Grave Creek	SCU	0.73307	0.73184 (0.00235)	5
	Mark Creek	RBT	0.73869	0.74212 (0.00055)	5
	Mathew Creek	WCT	0.75032	0.74816 (0.00113)	5
	Norbury Creek	RBT	0.74765	0.74522 (0.00100)	5
	Perry Creek	SCU	0.75958	0.76109 (0.00030)	5
	Sand Creek	SCU	0.71905	0.71833 (0.00033)	4
	Skookumchuck Creek	SCU	0.74382	0.74406 (0.00049)	4
	St. Mary River Lower	SCU	0.73925	0.74020 (0.00257)	5
	St. Mary River Upper	SCU	0.74226	0.74299 (0.00030)	5
	Tobacco River	SCU	0.72866	0.72929 (0.00094)	5
	Wigwam River	WCT	0.72474	0.71357 (0.00534)	5
	Wild Horse River	SCU	0.72383	0.72454 (0.00095)	4
	Region Mean[c]		0.73680	0.73679 (0.01285)	70
	SD		0.01180		

Note: Regional means without letters in common are significantly different. Standard deviations (SD) for water $^{87}Sr/^{86}Sr$ are indicated below the regional mean and for otolith $^{87}Sr/^{86}Sr$ in parentheses. Species designations are Bull trout (BLT), Sculpin (SCU), Redside shiner (RSS), Rainbow trout (RBT) and Cutthroat trout (WCT).

(2σ; $n = 8$) compared to the certified value of 0.71034 ± 0.00026 (NIST, 2007).

Following laser ablation, the transects across the otolith were photographed with a digital camera (Infinity 1, Lumenera) and the distance from the core to the otolith edge was measured using Image Pro software and the Otolith M application (MediaCybernetics; www.mediacy.com) (Figure 2). The total age was determined from visible annuli between the core and otolith edge and measurements of each annulus across the laser ablation path were recorded. These measurements were then used to classify age at first movement (if any) across the otolith. Because most Burbot were caught from late fall to early spring, otolith growth after annulus formation was not

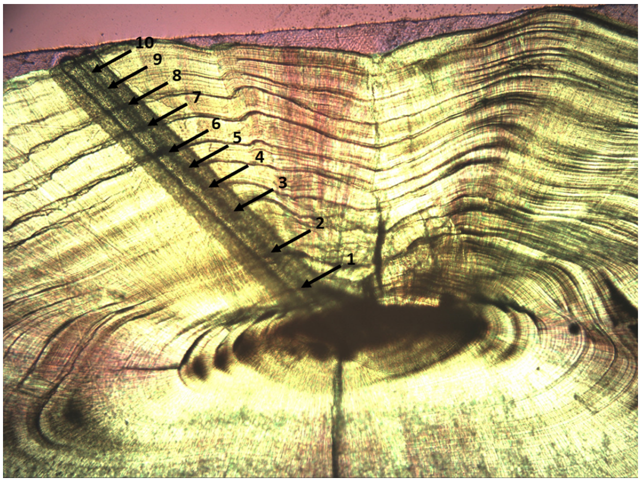

FIGURE 2 Representative Burbot otolith showing laser ablation path and annuli (labelled in black).

included in the age determination. We assigned a year class to each Burbot by subtracting the estimated age from the year of capture.

2.3 | Data analysis

Differences in water and surrogate fish otolith $^{87}Sr/^{86}Sr$ among the main geologic formations and boundary region (Table 1) were determined by analysis of variance (ANOVA) and Tukey's range test. This test served as the basis for constructing a classification model to determine the regions of natal origin for archived otolith samples of Burbot collected in Lake Koocanusa. Values of $^{87}Sr/^{86}Sr$ were assigned to individual surrogate fish and Burbot by first plotting the data from each laser transect in relation to distance from the otolith core to determine if distinct changes in $^{87}Sr/^{86}Sr$ could be identified indicating possible movement between waters of differing $^{87}Sr/^{86}Sr$. For samples that showed no evident change in $^{87}Sr/^{86}Sr$, the assigned value was calculated as the average of data acquisitions within the entire laser transect. For fish that exhibited apparent movement, a regression tree procedure (JMP Software, SAS Institute) was used to identify changes along the ablation path that represented significantly different $^{87}Sr/^{86}Sr$ segments. The procedure is similar to global zoning algorithms and segmented regression for identifying systematic shifts in otolith isotopic and elemental ratios by division into chemically homogenous zones (Hegg et al., 2019; Walther et al., 2011). We used the procedure to constrain the selection of otolith $^{87}Sr/^{86}Sr$ data representing natal stream origin. Details for the regression tree analysis of otolith $^{87}Sr/^{86}Sr$ can be found in Janak et al. (2021). The region of origin for surrogate fish and Burbot that displayed apparent movement was determined from the mean of the data within the first homogenous segment approximately distal to the first feeding check marking the extent of maternal influence in the otolith core (Brennan et al., 2015; Hegg et al., 2019). Representative examples of the procedure applied to individual fish are shown in Figure 3. Any apparent movement between the mainstem Kootenai River and a tributary stream later in life was identified visually across the transect and paired with the age data to characterise age at movement.

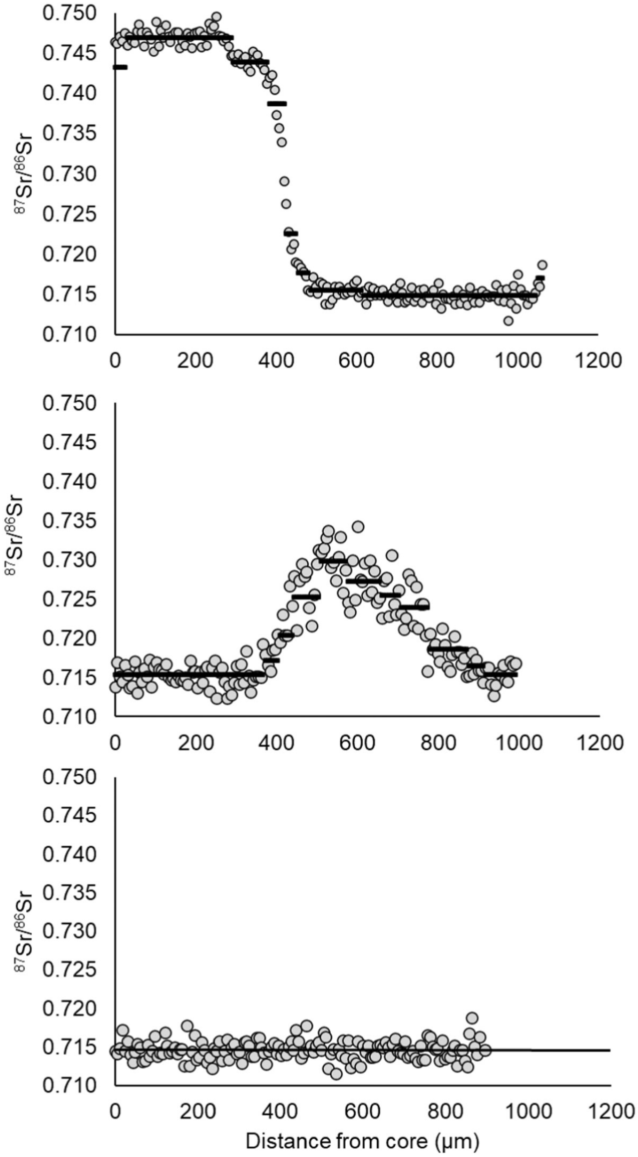

FIGURE 3 Representative examples of putative migratory (top and middle panels) and resident (bottom panel) life history forms of Burbot in Lake Koocanusa. Solid lines are homogenous segments of otolith $^{87}Sr/^{86}Sr$ determined by regression tree analysis.

Prior to analysis, the data for water, surrogate fish and archived Burbot otolith $^{87}Sr/^{86}Sr$ were examined for normality and equality of variances among the sample regions. Water and surrogate fish otolith $^{87}Sr/^{86}Sr$ were not normally distributed (Shapiro–Wilk test $p < .001$) and the variances were also unequal (Levene's test, $p < .001$). Because the data could not be transformed to meet these assumptions, differences in water and otolith $^{87}Sr/^{86}Sr$ among the geologic regions were determined by Kruskal–Wallis analysis of ranks test and Conover – Inman pairwise comparisons. The level of significance for all tests was $\alpha \le .05$.

Random forest (RF) classification was used to assign the archived Burbot otolith samples to their presumptive origins in the Kootenai River mainstem or the Palaeozoic and Proterozoic geologic formations. Random forest is a machine-learning method based on classification trees that have been used for provenance studies of fish involving both multi- (Tournois et al., 2017) and single-variate (Willmes et al., 2021) otolith markers. An important feature of RF is that it does not require the assumption of normal distribution for the data, and it has been shown to provide higher assignment accuracy compared to other classification methods (Mercier et al., 2011). The procedure recursively splits the data by bootstrapping with replacement to construct trees comprised of a random subset of the training and test samples. Otolith ^{87}Sr/^{86}Sr data from the surrogate fish samples were used to build, train and test the model. A total of $n = 500$ trees were built using 80% of the data to build and train the model and 20% to test the model. A cross-validation procedure was applied to evaluate the prediction accuracy (i.e., percentage of correct assignment to their origin). The model was then used to predict the natal region of origin for the Burbot collection from Lake Koocanusa based on the ^{87}Sr/^{86}Sr in the archived otolith samples.

The putative natal region assignments for the Lake Koocanusa Burbot were further analysed for their contribution to historic gill net surveys conducted by MFWP. These standardised surveys began in 1975 and have provided estimates of relative abundance expressed as catch per unit effort (CPUE; Burbot per net) (Dunnigan et al., 2021). They have occurred annually except in 1977, 1979 and 1983 when there was no sampling. The inter-annual variation in the CPUE for the sampling areas was plotted based on the collection year and year class estimated from age and fit with a 5-year moving average trend line to assess the relationship between the region of natal origin and year of hatch. We chose a 5-year moving average for the trend line because this time frame aligned well with the mean age of Burbot.

3 | RESULTS

Water ^{87}Sr/^{86}Sr varied widely among individual sample sites, ranging from 0.70889 in the Middle Fork of the White River to 0.75958 in Perry Creek (Table 1), and the differences were significant among each of the geologic regions ($K = 28.91$, $p < .001$). Surrogate fish were comprised of Columbia Slimy Sculpin (72.5%), Redside Shiner (10.6%), Rainbow Trout (7.0%), Westslope Cutthroat Trout (7.0%) and Bull Trout (2.8%) (Table 1). Otolith ^{87}Sr/^{86}Sr in surrogate fish samples closely approximated water ^{87}Sr/^{86}Sr at most sample sites and the relationship between water, and the mean otolith ^{87}Sr/^{86}Sr was highly significant ($F_{1,28} = 1057.8$, $p < .001$, $R^2 = 0.97$) (Figure 4). The lowest ratio (0.70898 ± 0.00025) came from Slimy Sculpin in the Middle Fork of the White River, whereas the Sculpin in Perry Creek were the highest (0.76109 ± 0.00025). The outlier in Figure 4 was produced by Cutthroat Trout in the Wigwam River that may have included recent immigrants from a nearby Palaeozoic formation stream (e.g. Elk River). Kruskal–Wallis analysis also indicated that otolith ^{87}Sr/^{86}Sr of the surrogate fish differed significantly among the regions ($K = 116.12$, $p < .001$) and the ratio for each region was significantly different from the others ($P \leq .003$).

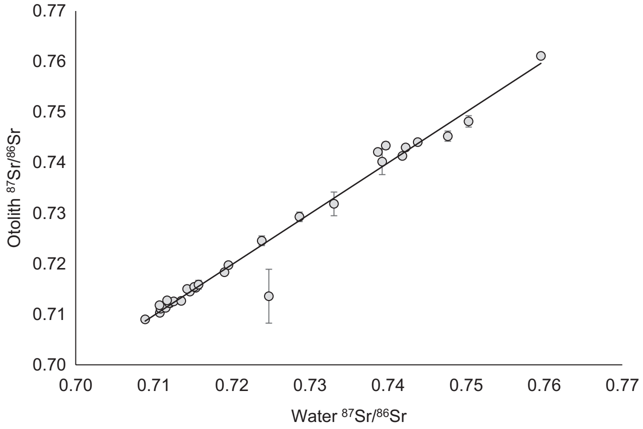

FIGURE 4 The relationship ($y = 1.006x - 0.004$) between water and otolith ^{87}Sr/^{86}Sr in resident fish from 30 sample sites in the upper Kootenai River watershed. Error bars are standard deviations and smaller than the symbol width for most sites.

The RF classification resulted in high assignment accuracy for both surrogate fish and Burbot to their known and presumptive natal regions, respectively. The RF cross-validation procedure correctly assigned approximately 92.7% of the learning samples and 100% of test samples from surrogate fish to their origins in the Kootenai River mainstem and adjacent geologic formations (Table 2). The surrogate fish RF model assigned $n = 2$ Burbot to the Palaeozoic formation, $n = 77$ to the Kootenai River mainstem and $n = 68$ to the Proterozoic formation (Table 3). Burbot originating in the Kootenai River mainstem dominated the archived samples in the brood years during the 1970s and after 2000, whereas those that recruited in the 1980s and1990s appeared to have originated largely from streams in the Proterozoic formation. Given the wide differences in water and otolith ^{87}Sr/^{86}Sr of the surrogate fish, the mean (± SD) assignment probabilities for all Burbot combined approached unity ($p = .996 \pm .033$). The high assignment probabilities for the Burbot were also reflected in the otolith core ^{87}Sr/^{86}Sr for the respective regions. Burbot otolith core ^{87}Sr/^{86}Sr showed a largely bimodal distribution, where most of the samples were clustered around either ~0.715 or ~0.74–0.75 (Figure 5). Burbot assigned to the Palaeozoic formation had the lowest ratio (0.71339 ± 0.00089), those from Proterozoic tributaries were the highest (0.74769 ± 0.00530) and mainstem fish were intermediate (0.71500 ± 0.00039).

The age structure for the Burbot collected in Koocanusa Reservoir from 1980 to 2016 is shown in Figure 6. The mean estimated age ± SD for all fish from 1980 to 2016 was 5.8 years ±1.8 and individual ages ranged from 3 to 12 years. The sample distribution was dominated by fish of age 5 and age 6 from 1980 to 1999, then shifted to a more even distribution from 2000 onward that were mostly from age 4 to 7. The mean age of Burbot that originated from the mainstem and Proterozoic formation tributaries did not differ

TABLE 2 Confusion matrix from cross-validation (n = 10) assignment of surrogate fish (n = 138) to their natal region for the random forest model. Values are for the training and (test) samples, respectively.

	Palaeozoic	Mainstem	Proterozoic	% Accuracy
Palaeozoic	31 (10)	0 (0)	4 (0)	88.5 (100)
Mainstem	0 (0)	18 (6)	0 (0)	100 (100)
Proterozoic	4 (0)	0 (0)	53 (12)	92.9 (100)
Total	35 (10)	18 (6)	57 (12)	92.7 (100)

TABLE 3 Random forest model assignment of burbot collected in Lake Koocanusa by decade of brood year to their putative natal region of origin.

	1970–1979	1980–1989	1990–1999	2000–2012	Total
Palaeozoic	0	0	1	1	2
Mainstem	24	18	10	25	77
Proterozoic	4	38	23	3	68
Total	28	56	34	29	147

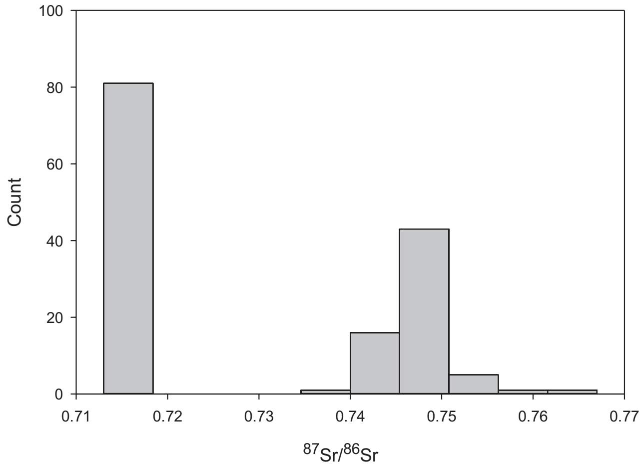

FIGURE 5 Frequency distribution of otolith core ^{87}Sr/^{86}Sr from adult Burbot collected in Lake Koocanusa between 1980 and 2016.

significantly during the 1980s or 1990s ($K \leq 0.51$, $p \geq .48$), but Burbot originating in the mainstem were significantly older during the period from 2000 to 2016 ($K = 7.55$, $p = .006$).

The major life history forms of Burbot (Figure 3) are summarised by decade in Figure 7. Burbot originating in tributary streams of the Proterozoic (top panel Figure 3) and Palaeozoic formations that migrated to and remained resident in the mainstem represented the most abundant form (n = 70), with the majority of these fish showing movement in their first year (median age = 0, range = 0–2). Of these fish, roughly half (n = 36) moved in a gradual fashion through relatively lower ^{87}Sr/^{86}Sr water before entering the mainstem in their second year (median age = 1, range = 0–3) and a small number (n = 5) showed evidence of a return to higher ^{87}Sr/^{86}Sr water (median age = 2, range = 0–5) before final movement back into the mainstem. Burbot that originated in and remained resident in the mainstem (bottom panel Figure 3) represented the second most abundant form (n = 65). The least abundant form (n = 13) was a variant that showed apparent origin in the mainstem, followed by movement into higher ^{87}Sr/^{86}Sr water (Proterozoic formation tributaries) between the age of 0 and 5, and eventual return to the mainstem (middle panel Figure 3). These life history patterns shifted over time, most notably from 1980 to 1999 when the tributary-origin forms were dominant, in contrast to the more abundant mainstem-origin Burbot collected during the 1970s and 2000s. This shift in natal origin over time was also evident in site assignment by RF (Table 3).

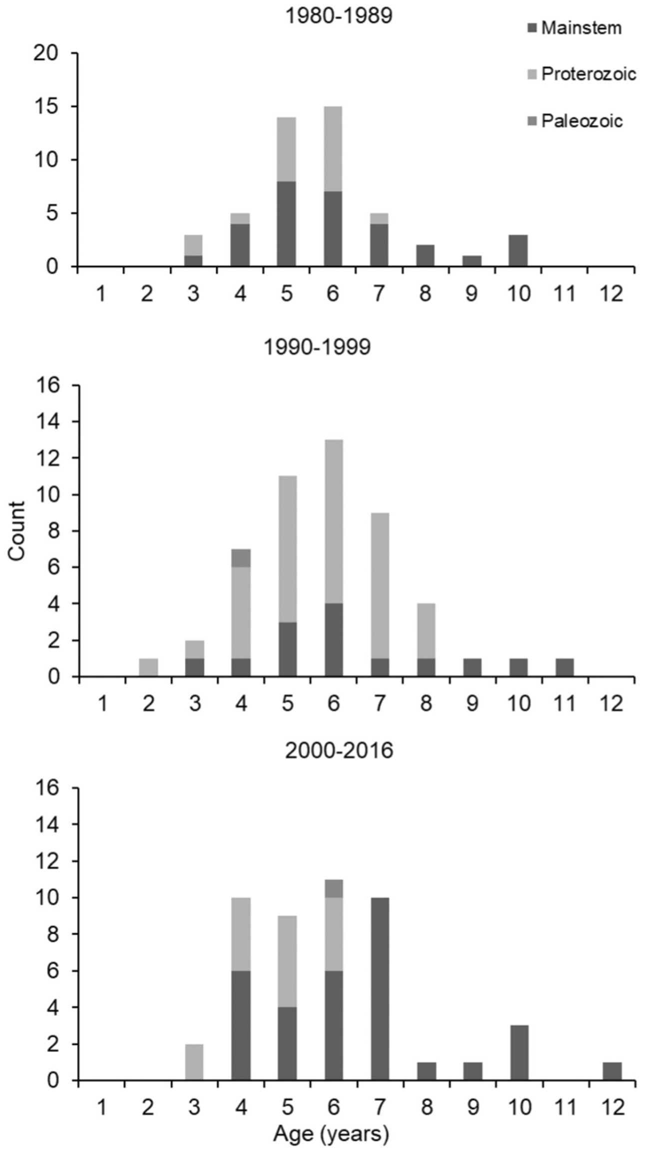

FIGURE 6 The age distribution and natal region assignment of Burbot from Lake Koocanusa collected from 1980 to 2016.

The CPUE for mainstem-origin Burbot increased rapidly after 1975, peaking at 0.51 fish per net in 1980, then declined slowly over the following 30 years (Figure 8). This trend is also evident in the 5-year CPUE moving average. By comparison, the CPUE for tributary-origin Burbot increased more slowly after 1975 until reaching a maximum (0.68 fish/net) in 1988, then exhibited a similar decline during the next 20 years, falling to near zero after 2005. There were only three Burbot in our study assigned to the Proterozoic region that has hatched since 2000, the most recent being a 4-year-old fish captured in 2010.

4 | DISCUSSION

Burbot populations have been adversely affected by human activity across wide parts of their circumpolar distribution and habitat changes from the construction and operation of hydropower dams have been implicated as a major cause (Harrison et al., 2016; Stapanian et al., 2010). Evidence suggests Burbot abundance in the Kootenai River decreased because of similar changes, and while these have been well documented for the population downstream of Libby Dam (Hardy et al., 2015), the reasons for decline above the dam are less understood. To help address this knowledge gap, we reconstructed natal origin, habitat use and life history structure of Burbot from $^{87}Sr/^{86}Sr$ variation in archived otoliths collected over four decades in Koocanusa Reservoir and in contemporary samples of water and surrogate fish otoliths from the upper Kootenai River. Our results indicate that Burbot caught during abundance surveys in the reservoir were recruited primarily from two locations: (1) the mainstem of the Kootenai River and (2) from tributaries originating in the sedimentary Proterozoic rocks that dominate the western and southern parts of the upper basin. Contributions from both sources first increased and then decreased after inundation, but not in synchrony. Mainstem river Burbot were dominant in the surveys in the 1970s and after 2000, while catches in the 1980s and 1990s originated mostly from tributary streams. The mean age at capture changed little over time, and the only difference between the mainstem and the tributary sources was from 2000 onward. Most notably, otolith $^{87}Sr/^{86}Sr$ showed limited evidence of tributary-origin Burbot returning to their natal region.

Our ability to assign archival otolith samples of Burbot from Koocanusa Reservoir to their putative region of natal origin benefitted from the range in water $^{87}Sr/^{86}Sr$ that reflected the substantial geological variation within the upper Kootenai River watershed, in some cases, at fine spatial scales. For example, Norbury Creek (0.74765) and the Bull River (0.71153) enter the Kootenai River from the east within approximately 1.5 km of each other (Figure 1). The Bull River drainage lies largely on a boundary between sedimentary rocks of Lower and Upper Palaeozoic age (~500–250 Ma), whereas Norbury Creek originates from a band of sedimentary rock from the Middle Proterozoic that dominates much of the basin (~1500–1000 Ma). More generally, however, water $^{87}Sr/^{86}Sr$ values are consistent with the geologic age of the formations they drain from. Water $^{87}Sr/^{86}Sr$ at sites originating from the Palaeozoic and Mesozoic sedimentary rocks in the northeastern portion of the basin are well below those of the Kootenai River mainstem and the older

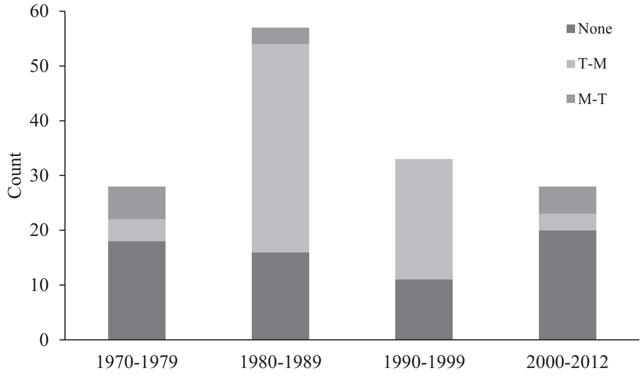

FIGURE 7 The number of Burbot in each movement category by the decade of recruitment to the population. The most recent and youngest Burbot (age 4) was collected in 2016. Movement categories are resident mainstem (none), tributary to mainstem (T–M) and mainstem to tributary (M–T). Representative otolith $^{87}Sr/^{86}Sr$ transects for each category are shown in Figure 3.

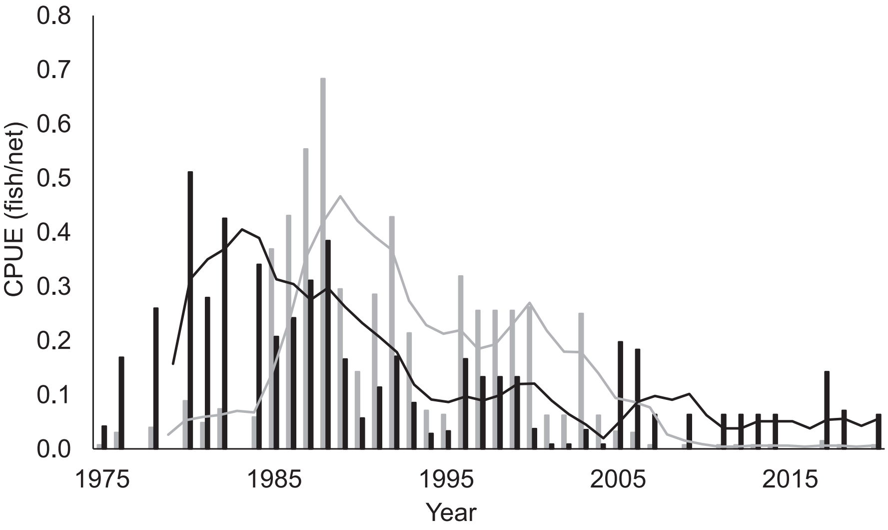

FIGURE 8 Relative abundance of Burbot in Koocanusa Reservoir from 1975 to 2020 indexed by standardised catch per unit effort (CPUE) that assigned to the mainstem (black) and Proterozoic (grey) regions by RF analysis. Trend lines were fit using a 5-year moving average. Sampling was not conducted in 1977, 1979 and 1983. CPUE for the years without data indicate *n* = 0. Burbot (*n* = 2) from the Palaeozoic region is not shown.

Proterozoic formations (Table 1). There were, however, several exceptions to this pattern. For instance, Gold Creek originates west of the Kootenai River mainstem and flows entirely through sedimentary Proterozoic rock yet had a comparatively low water $^{87}Sr/^{86}Sr$ (0.71955) for this formation. Similarly, the Tobacco River (0.72866) and Grave Creek (0.73307) also exhibited high water $^{87}Sr/^{86}Sr$ indicative of the Proterozoic era formation, but these appear to drain mostly through Quaternary outwash (2.5 Ma to present) and may reflect natural reworking of older material into these deposits.

We used a random forest model to classify Burbot to their geological region of origin based on the $^{87}Sr/^{86}Sr$ in otolith samples collected from several fish species that we assumed were mostly, if not entirely, resident in the streams and rivers within these regions. The use of otoliths from surrogate species to train classification models or relate unknown samples to specific waters has been demonstrated elsewhere (Brennan et al., 2015). Sculpin, in particular, have shown utility for this purpose because of their limited home range (Brennan et al., 2015; Gray et al., 2018) and our data support these findings (Figure 4). However, otolith $^{87}Sr/^{86}Sr$ in other species that included Redside Shiner, Bull Trout, Rainbow Trout and Cutthroat Trout also showed a high correlation and nearly 1:1 correspondence with water $^{87}Sr/^{86}Sr$ from their respective sample sites, which further confirmed our assumption of stream residence and use of these fish as surrogates to train the RF model. The only exception to this relationship came from the samples of Cutthroat Trout collected in the Wigwam River that appeared to have migrated from a stream system with lower water $^{87}Sr/^{86}Sr$ (Table 1). This relationship and the wide variation in water $^{87}Sr/^{86}Sr$ among the sample sites from the Kootenai River and adjoining tributaries resulted in high, cross-validated assignment accuracy of resident fish to their natal geologic regions. The archived otoliths of Burbot collected in Lake Koocanusa were similarly classified to these sites with high assignment accuracy based on early life $^{87}Sr/^{86}Sr$ transect data. Although we acknowledge that site assignments could have been misclassified by larval Burbot moving from tributary to mainstem habitats before incorporating natal stream $^{87}Sr/^{86}Sr$, the early life history behaviour suggests that this is unlikely. Burbot larvae initiate swim bladder inflation and first feeding about 10–12 days after hatching (Egan et al., 2015) and exhibit pelagic behaviour until seeking benthic cover at about 68 days post-hatch (Jude et al., 2013). By comparison, strontium isotopes in otoliths reach equilibrium with ambient water after approximately 3 weeks (Munro et al., 2008), indicating that in most cases, there should have been sufficient time to acquire a natal stream signature.

Our findings, along with historical and contemporary records of spawning activity, suggest that the St. Mary watershed was the most likely origin of the majority of Burbot that were classified into the Proterozoic formation (Cope, 2019). The mean ± SD (0.74760 ± 0.00379) and range (0.73814–0.76597) in otolith $^{87}Sr/^{86}Sr$ of Burbot that assigned to this region were nearly identical to the water $^{87}Sr/^{86}Sr$ of the upper and lower St. Mary River and tributaries within the watershed such as Mark Creek, Matthew Creek and Perry Creek (Table 1). Interestingly, although the Bull River and Elk River have been identified as providing favourable spawning and rearing habitat for Burbot and were historically important harvest locations (Cope, 2019), our evidence indicates that contributions to the Lake Koocanusa population from these and other Palaeozoic formation tributaries was negligible. Rather, these fish may represent a resident form localised to these rivers or that they migrate to areas in the upper Kootenai River other than Lake Koocanusa.

Developing recovery strategies for species of conservation concern requires a fundamental understanding of the organism's life history. Prior to our study, little was known about upper Kootenai River Burbot life history including natal origin or trends in abundance based on their origin. Filling such information gaps is a prerequisite for postulating causes of change in population abundance that can help guide management actions for recovery. For example, determining periods of abrupt decline for mainstem- or tributary-origin Burbot in the upper Kootenai River could be useful for identifying concurrent alterations in water or land use practices that may have contributed to those declines. Studies of Burbot across their circumpolar range indicate these activities and their effects have been variously related to entrainment, trophic depression and pollution (Harrison et al., 2016; Stapanian et al., 2010). Entrainment, the involuntary downstream passage at dams through spillways and powerhouses, can remove fish from reservoirs at all life stages. Adult Burbot may be vulnerable to hypolimnetic turbine entrainment because of their benthic orientation (Dunnigan & Sinclair, 2008; Harrison et al., 2016;). They are also physoclistous and cannot quickly expel air from their swim bladder, which increases their risk of barotrauma injury because of rapid decompression during turbine passage (Brown et al., 2014). The problem is exacerbated in Burbot acclimated to deeper water due to the greater air pressure within the swim bladder (Bruesewitz et al., 1993). However, the extent to which adult Burbot are negatively impacted by entrainment has varied widely. Annualised estimates of population entrainment from tagging studies have ranged from ~1 to 32% and have been confounded by small sample sizes and differences in study duration (Dunnigan & Sinclair, 2008; Martins et al., 2013; Spinelli, 2010). Dunnigan and Sinclair (2008), for example, reported that of 40 adult Burbot tagged in Lake Koocanusa, only one was entrained at Libby Dam over 18 months of observation, representing a 1.6% annual removal rate. Pre-settlement life stage Burbot may also be susceptible to entrainment because of passive drifting by post-hatch larvae and weak swimming ability of pelagic phase juveniles (Wang & Appenzeller, 1998). In Lake Koocanusa for instance, the continued decline in the CPUE for both mainstem- and tributary-origin Burbot from the 1990s onward coincided with changes in reservoir management to aid the recovery of White Sturgeon *Acipenser transmontanus* in the lower Kootenai River (USFWS, 1994; 59 FR 45989). These included increased spring storage volume in Lake Koocanusa and higher discharge below Libby Dam that reduced hydraulic residence time in the reservoir by approximately 50% (US ACOE, 2021; USFWS, 1995) during and after the time of Burbot hatch (Ashton et al., 2019). Entrainment losses of early life stage Burbot at Libby Dam have not been determined but estimates of annual removal in other species with similar pelagic residence (e.g. age 0+ Kokanee salmon, *O. nerka*) have ranged from approximately 1–4 million fish (Skaar et al., 1996), suggesting potential losses of larval and juvenile Burbot as well.

Reservoirs formed by dams can also undergo changes in water quality (Baxter, 1977) and nutrient availability (Hu et al., 2012; Woods, 1982) after inundation. Flooding of upland areas transports organic matter and nutrients from vegetation and soils, increasing the biomass of planktonic and pelagic fish communities (DesLandes et al., 1995; Paterson et al., 2019) that are the main dietary sources of early feeding and post-settlement phase Burbot, respectively (Ghan & Sprules, 1993; Schram et al., 2006; Wang & Appenzeller, 1998). This 'trophic upsurge' (Ostrofsky, 1978) typically declines afterwards as the available nutrients are consumed or lost to sediment deposition (Seitzinger et al., 2002; Wollheim et al., 2006). Phosphorus is an essential trace element for phytoplankton production in the water column (Goldman & Horne, 1994) and a major factor controlling the magnitude and duration of the trophic surge in reservoirs (Paterson et al., 2019). Pre-inundation measurements in Lake Koocanusa are not available, but records indicate a reduction in total phosphorous by several orders of magnitude since the early 1970s (MT DEQ, 2021; USGS, 2021). The high concentrations shortly after inundation likely included inputs from flooded land as well as industrial activity in the St. Mary River before reservoir formation (Cope, 2019). We suggest that these sources could have contributed to higher zooplankton abundance and hence juvenile survival (Ghan & Sprules, 1993; Wang & Appenzeller, 1998) for the decade after inundation, and attenuation thereafter, in general agreement with the CPUE change for mainstem-origin Burbot in the abundance surveys (Figure 7).

Finally, pollution has negatively impacted many Burbot populations, particularly in Europe (Stapanian et al., 2010) and inputs of metals and other contaminants in the Kootenai River basin may have been important in the abundance dynamics of Burbot within the Kootenai watershed. Industrial discharges in the St. Mary River date to the early 1900s, and although abatement efforts that began in the 1970s have largely eliminated these contributions (Cope, 2019), there has been a nearly 5-fold increase in selenium (Se) concentrations from 1986 to present in the Elk River (Palaeozoic region; Figure 1) which contributes on average 26% of the annual inflow to Lake Koocanusa (Environment Canada, 2022). Evidence indicates the major source of this enhanced Se has been coal mining in the Elk River basin, which contains abundant Se-bearing strata (Cooke & Drevnick, 2022; Friedrich et al., 2011; Wellen et al., 2015). Selenium is an essential micronutrient for many biological functions, but high concentrations can have severe, detrimental effects on ovaries in fish and produce deformity and mortality in fish larvae through maternal transfer (Lemly, 2002). Rudolph et al. (2008), for example, found that eggs of Cutthroat trout from the Elk River with elevated Se concentrations (>47 μg/g dry weight) failed to produce viable fry, and at higher concentrations were either non-viable at fertilisation or could not be successfully fertilised. Moreover, Orr et al. (2012) reported that these high concentrations of Se in Elk River Cutthroat trout appeared to result from bioaccumulation through the benthic food chain, particularly in lentic habitats, suggesting that benthic-oriented species such as Burbot could experience similar if not greater effects on reproduction. Contemporary samples of Burbot egg and ovary tissue from Lake Koocanusa and the Kootenai River downstream of Libby Dam that frequently exceed Environmental Protection Agency guidelines for Se support this inference (S. Young, Kootenai Tribe of Idaho, personal communication).

Impaired maturation could also explain the apparent migratory failure among putative tributary-origin adults (Figure 3, top panel). Burbot reportedly migrate to specific spawning sites with high synchrony and high site fidelity (Paragamian & Wakkinen, 2008), but our data contrast with these findings. Although most of the otoliths we analysed for $^{87}Sr/^{86}Sr$ revealed prevalent movement from Proterozoic formation tributaries into Lake Koocanusa, there was limited evidence of return migration. Apparent movement by mainstem-origin Burbot into tributary streams was also rare. Telemetry studies conducted on this population in the early 2000s support these conclusions (Dunnigan & Sinclair, 2008). If tributary-origin Burbot undertook spawning migrations from the Kootenai River mainstem to their natal streams in the Proterozoic formation, this movement should have been recorded in otolith $^{87}Sr/^{86}Sr$. As we noted previously, fluvial forms of Burbot can make spawning migrations of considerable distance and duration and may remain in the vicinity of their spawning grounds for a month or more (Jude et al., 2013; McPhail & Paragamian, 2000; Paragamian & Wakkinen, 2008). Due to the wide differences in water $^{87}Sr/^{86}Sr$ between the Kootenai River and the Proterozoic formation tributaries (Table 1), and the duration of time needed for otolith–water strontium isotope equilibrium (Munro et al., 2008), changes in otolith $^{87}Sr/^{86}Sr$ should be evident if these tributary-origin adults rearing in the mainstem returned to higher $^{87}Sr/^{86}Sr$ water to spawn. Additionally, all the otolith samples analysed were from Burbot of potential reproductive age (range 3+ to 12+ years), and because most are annual spawners (McPhail & Paragamian, 2000), there should have been ample opportunity for these fish to have undertaken spawning migrations. This suggests that the tributary-origin Burbot that migrated to Lake Koocanusa may have remained there to spawn, or if they returned to their natal tributary sites, they did not make subsequent migrations back to the reservoir. However, we recognise that such behaviour could be natural to this population, that is resident life history forms that give rise to migratory offspring. Similar behavioural plasticity has been reported for Rainbow Trout (Zimmerman et al., 2009) and could also exist in Burbot. Hardy et al. (2015) reported that lacustrine broodstock (Moyie Lake, B.C.) used for Burbot supplementation in the lower Kootenai River produced fluvial progeny and suggested that this was evidence of adaptive plasticity in the species to survive in various habitats irrespective of parental origin.

In summary, the Burbot population in the upper Kootenai River followed a pattern of increasing then declining abundance after the construction of Libby Dam, similar to the trend observed in the lower river population. Analysis of otolith $^{87}Sr/^{86}Sr$ from archival samples collected over four decades revealed that the population in Lake Koocanusa was comprised of both tributary- and mainstem-origin Burbot and that the contributions of these forms changed over time, possibly in response to anthropogenic impacts associated with the dam and other activities in the watershed. Our findings also showed a wide disparity in contributions of tributary-origin Burbot between the Proterozoic and Palaeozoic regions to the abundance surveys in Lake Koocanusa. The reasons for this difference are unknown, but it could reflect higher concentrations of naturally occurring Se or other metals in streams within the Palaeozoic region that potentially impair the reproduction or survival of larval Burbot.

We suggest several lines of inquiry to resolve questions raised by our study. First, analyses of otolith^{87}Sr/^{86}Sr from Burbot caught in the St. Mary River would provide needed information regarding their migratory behaviour and life history form(s). This population historically represented a large component of the Burbot harvested in Lake Koocanusa and better knowledge of their movement(s) and reproductive strategies would improve understanding of regional population dynamics. Second, analyses of Se concentrations in archived otoliths of Burbot from Lake Koocanusa are required to determine exposure history in the reservoir. Selenium exposure profiles have been established for multiple species in the Elk River other than Burbot, and these show considerable variability in concentration, timing and frequency (Friedrich et al., 2011). Combined with tissue and otolith Se concentrations in contemporary Burbot samples and performed in conjunction with replicated and controlled toxicology studies, these retrospective analyses could yield information about the potential long-term impacts of coal mine discharges to establish water quality criteria appropriate to protect and rebuild the upper Kootenai River population(s). Third, it would be beneficial to determine the extent that changes in hydro operations have influenced entrainment and food availability of early life history Burbot at Libby Dam. The timing of the decline of the mainstem-origin Burbot generally coincides with operational changes at Libby Dam during the spawning and larval life stages of Burbot. Unpublished data indicate a significant correlation between the CPUE for mainstem-origin Burbot and the hydraulic residence time of Lake Koocanusa that characterises the operational changes at Libby Dam (J. Dunnigan, personal communication). Quantifying the effects of hydro operations on Burbot early life history survival and abundance would aid assessments of how Lake Koocanusa water storage and release might be managed for multi-species benefit.

AUTHOR CONTRIBUTIONS

J.M.J and M.K.N performed the sample analyses; T.J.L. and L.G. analysed the data with assistance from J.M.J and M.K.N; J.L.D. and G.A.M. supervised the project. All authors contributed to writing the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts or competing interests.

DATA AVAILABILITY STATEMENT

Data used in the study will be made available on request to the Montana Fish, Wildlife and Parks.

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