Articles

Natal Contributions of Kokanee Salmon to Flaming Gorge Reservoir, Wyoming–Utah: An Evaluation Using Otolith Microchemistry

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Abstract

In a system that uses supplemental stocking to enhance a fishery that serves a dual purpose, an understanding of the contributions from natural and hatchery-produced fish is important so that hatchery resources can be appropriately allocated. Kokanee *Oncorhynchus nerka* were first stocked in Flaming Gorge Reservoir (FGR), Wyoming–Utah, in 1963 and serve a dual purpose as a prey resource and sport fish. Although natural recruitment occurs in the reservoir, a supplemental stocking program was initiated in 1991. We sought to identify the natal origin (i.e., natural, hatchery) of kokanee in FGR using otolith microchemistry. We evaluated return to the creel, composition of spawning aggregates, and growth of kokanee in FGR and focused on differences associated with natal origin. We analyzed kokanee otoliths that we collected from hatcheries ($n = 60$) and FGR ($n = 1,003$) for the strontium isotope ratio, $^{87}Sr/^{86}Sr$, using laser ablation and a multicollector inductively coupled plasma mass spectrometer. We conducted Kruskal–Wallis tests to compare the strontium isotope ratios from the otolith edge of kokanee that we sampled from hatcheries and FGR. Based on $^{87}Sr/^{86}Sr$ ratios, we could distinguish natural-origin kokanee from 11 of the 12 hatcheries ($P < 0.01$); however, the Wigwam Hatchery was not significantly different from FGR ($P = 0.84$). We used model-based discriminant function analysis to assign natal origins for kokanee caught in FGR. Hatchery contribution to the population at large varied from 21 to 50% among year classes from 2014 to 2018. The percentage of hatchery origin kokanee in the creel (18–50%) was similar to what we observed in the population. Hatchery-produced kokanee contributed a higher proportion to tributary-spawning aggregates (40–90%) than shoreline-spawning aggregates (19–58%) by sample year. Growth of natural and hatchery kokanee was similar, suggesting similar performance in the system. Results from this study identify that hatchery supplementation contributes to the population and recreational harvest of kokanee in FGR. This research also provides insight into the ecology of kokanee that is useful for better understanding kokanee population dynamics in reservoir systems.

The findings and conclusions in this article are those of the author(s) and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

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Introduction

Stocking efforts to maintain or enhance a fishery can be challenging and costly for natural resource agencies (Yule and Luecke 1993; Martinez and Wiltzius 1995; Johnson and Martinez 2000). In systems that use stocking to supplement natural production, an understanding of the contributions from natural and hatchery-produced fish is important so that hatchery resources can be efficiently allocated. In western lakes and reservoirs, introduced kokanee *Oncorhynchus nerka* often serve as both a sport fish and prey resource (Wydoski and Bennett 1981; Martinez et al. 2009). Kokanee are nonanadromous Sockeye Salmon indigenous to northwestern North America and northeastern Asia (Nelson 1968). Kokanee are native to Alaska, Washington, Idaho, and Oregon in the United States and the Yukon Territory and British Columbia in Canada. Introduced kokanee populations can become self-sustaining, but supplemental stocking is often needed when used for dual purposes (i.e., prey and sport fish; Wydoski and Bennett 1981; Rieman and Myers 1992). Flaming Gorge Reservoir (FGR), Wyoming–Utah, is one of many western reservoirs where kokanee were introduced to serve a dual purpose.

Kokanee were first introduced to FGR in 1963 (Parsons and Hubert 1988a; Figure 1). After the initial stocking events in 1963 and 1964, the kokanee population was sustained primarily through natural recruitment until a supplemental hatchery program was initiated in 1991. The hatchery program was initially focused on augmenting kokanee abundance to serve as a prey species for Lake Trout *Salvelinus namaycush* (Yule 1992; Gipson and Hubert 1993). Kokanee in the reservoir spawn in the Green River, Sheep Creek, and various shoreline locations around the reservoir (Parsons and Hubert 1988a, 1988b; Gipson and Hubert 1993). In recent years, spawning was observed in the Henrys Fork River along with additional shoreline locations. Contributions of natural and hatchery-produced kokanee to the various spawning aggregates are unknown. Since initiation of the stocking program, the Wyoming Game and Fish Department (WGFD), Utah Division of Wildlife Resources, and U.S. Fish and Wildlife Service hatcheries have, on average, stocked 1,603,095 (SD of ±288,889) age 0 kokanee (i.e., fingerlings) annually (Table 1). Total length of stocked kokanee varied from 39 to 96 mm (74 ± 11 mm). The WGFD hatchery system annually produces about 1,200,000 kokanee, of which approximately 75% (900,000 age 0 kokanee) are stocked into FGR. In addition to the collaborative efforts to support a kokanee fishery, several studies have focused on habitat availability (Modde et al. 1997; Parsons and Hubert 1988a) and competition with Utah Chub *Gila atraria* (Schnei-

dervin and Hubert 1987; Teuscher and Luecke 1996). Furthermore, reproductive characteristics (Parsons and Hubert 1988b; Gipson and Hubert 1993), survival, abundance, distribution, and size structure of kokanee in FGR are known (Jeric 1996; Mosley et al. 2008). Despite these efforts, little is known about the relative contributions of natural and hatchery-produced kokanee to the population.

Maintaining an adequate balance between prey availability and harvestable fish in a system with supplemental hatchery production requires knowledge of differences in growth rates, natural recruitment, and harvest of natural and hatchery-produced fish (Yule and Luecke 1993; Martinez and Wiltzius 1995). Several methods are used to differentiate wild and hatchery
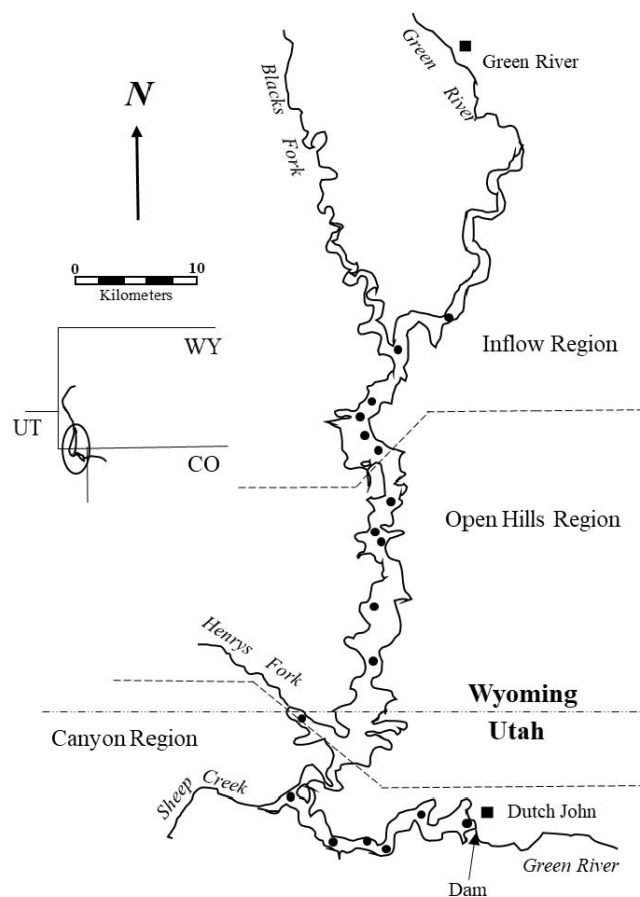

Figure 1. Flaming Gorge Reservoir, Wyoming–Utah, with major tributaries and regions of the reservoir based on bathymetric, limnological, and biological characteristics. Regions are separated by dashed lines. Black squares represent city centers for reference. Black circles indicate locations where we collected water samples in 2020.

Table 1. Kokanee *Oncorhynchus nerka* stocking records for Flaming Gorge Reservoir from 2013 to 2020. Agencies include Wyoming Game and Fish Department (WGFD), Utah Division of Wildlife Resources (UDWR), and U.S. Fish and Wildlife Service (USFWS). Hatcheries are separated by hatchery group (i.e., Auburn, Over, Under, "Natural") that we identified using a model-based discriminate function analysis based on similar $^{87}Sr/^{86}Sr$ ratios. The number stocked is the total number of kokanee stocked from an individual hatchery in a particular year. Mean length (total length) and average Julian stocking date values are averages from all stocking events of an individual hatchery each year. Annual contributions are the percentage of kokanee an individual hatchery contributed to Flaming Gorge Reservoir in a particular year.

Hatchery, agency	Year	Number stocked	Mean length (mm)	Average Julian stocking date	Annual contribution (%)
Auburn					
Auburn, WGFD	2013	168,320	66	134	17
	2014	446,892	65	141	29
	2015	310,906	88	139	19
	2016	381,600	85	154	29
	2017	559,260	73	150	30
	2018	389,010	100	159	27
	2019	345,266	57	142	19
	2020	259,254	73	140	20
Auburn Isolation, WGFD	2018	28,160	50	130	2
Over					
Boulder Isolation, WGFD	2014	29,040	68	136	2
Clarks Fork, WGFD	2017	137,840	88	137	7
	2019	130,440	80	129	7
Dan Speas, WGFD	2015	161,621	59	137	10
	2016	76,330	98	142	5
	2017	149,582	88	143	8
	2018	74,515	80	141	5
	2019	359,818	58	140	20
	2020	586,228	78	134	32
Under					
Daniel, WGFD	2013	81,432	53	150	8
	2014	66,720	72	152	4
	2015	88,823	60	132	5
	2016	87,619	50	142	6
	2020	9,075	99	125	1
Dubois, WGFD	2018	14,026	89	163	1
Jones Hole, USFWS	2013	359,400	82	127	37
	2014	354,609	83	124	23
	2015	439,697	82	149	37
	2016	282,442	88	148	19
	2017	341,664	85	151	19
	2018	338,920	88	150	21
	2019	592,389	95	150	32
	2020	437,029	87	153	24
Midway, UDWR	2017	64,080	76	96	3
	2018	48,342	46	115	3
Saratoga, USFWS	2013	80,800	65	140	8
Tillet, WGFD	2017	99,962	81	151	5
	2018	82,320	64	141	5
Whiterocks, UDWR	2013	281,860	82	114	29
	2014	665,500	76	107	43
	2015	622,201	87	86	38
	2016	442,392	83	105	29
	2017	362,575	80	117	27
	2018	439,880	68	114	27
	2019	392,568	81	124	22
	2020	432,620	86	128	24
"Natural"					
Wigwam, WGFD	2016	190,750	76	143	13
	2018	160,650	75	129	10

fish, including the use of chemical dyes and stains, stress-induced marks on otoliths, tags and marks, and otolith microchemistry (Paragamian et al. 1992; Kennedy et al. 1997). However, each identification method has limitations. Individuals may not absorb stains and dyes (e.g., oxytetracycline and casein) equally, and some compounds degrade when exposed to light (Paragamian et al. 1992). Hatcheries may not have resources required to induce stress marks (e.g., thermal marks; Paragamian et al. 1992; Volk et al. 1999). Also, stress marks can become difficult to identify in older fish without proper equipment (Paragamian et al. 1992). Removal of fins and/or implanting tags can be labor intensive, requires additional handling of fish, and may not be permanent (e.g., shed tags). Otolith microchemistry offers the unique potential to differentiate fish of different natal origins if the water chemistry is different between areas specific to the question(s) being asked (Kennedy et al. 2000). Although the use of microchemistry has limitations, advances in technology and in our understanding of applications have made it a reliable and effective tool for understanding the ecology of fishes (Kennedy et al. 2000; Campana and Thorrold 2001; Kennedy et al. 2002; Barnett-Johnson et al. 2008; Chase et al. 2015). In systems where the water chemistry of hatcheries differs from receiving waters, microchemistry serves as a tool to discriminate between natural and hatchery-produced fish. In fact, previous research showed that strontium isotope ratios (i.e., $^{87}Sr/^{86}Sr$) can be used to identify natal origin of kokanee (i.e., natural vs. hatchery) in FGR (WGFD, unpublished data).

Sagittal otoliths are the most commonly used hard structure for microchemistry analysis in fishes (Pracheil et al. 2014). Otolith microchemistry is useful for describing natal origin, life history variation, migration history, and stock discrimination through trace elements deposited in the otolith (Campana 1999; Thresher 1999; Kennedy et al. 2000, 2002; Barnett-Johnson et al. 2008). The environment-to-otolith pathway of ions starts with exchange at the gills or through ingestion where ions are transferred to blood plasma (Campana 1999; Payan et al. 2004; Whitledge 2017). Ions move from the blood plasma to the endolymph via active transport where each otolith is precipitated from the endolymphatic fluid. Otoliths are dominated by crystalline calcium carbonate, with the remainder being a noncollagenous matrix (Campana 1999; Long and Grabowski 2017; Whitledge 2017). Nearly 40 elements are present in otoliths, with most microchemistry studies reporting consistent assay of 5 to 10 elements (Thresher 1999).

Strontium is isostructural to calcium and is capable of substituting for calcium in biological structures (Kennedy et al. 2000; Campana and Thorrold 2001). Strontium isotopic ratios in bedrock persist in surface water and are derived from invariable geological sources (Fisher and Stueber 1976). The strontium isotopic ratios in surface water are stable among years, with potential for some level of seasonal variation (Kennedy et al. 2000, 2002; Brown and Severin 2009; Hegg et al. 2013). Even with seasonal variations, fish that reside in a region long enough to incorporate the chemical signature of the water can be distinguished from individuals among regions if chemical signatures of the regions are different (Kennedy et al. 2000; Heckel et al. 2020). We sought to use strontium isotope ratios derived from ambient water and sagittal otoliths to assess the natal origin of kokanee in FGR. In addition, we evaluated return to the recreational creel, composition of spawning aggregates, and growth of kokanee in FGR to assess differences based on natal origin.

Methods

Study area

Flaming Gorge Reservoir is located in southwestern Wyoming and northeastern Utah (Figure 1). The reservoir is formed by the impoundment of the Green River by Flaming Gorge Dam (completed in 1962) at Dutch John, Utah. The reservoir's primary purposes are water storage, flood control, hydropower, and recreation (Schneidervin and Hubert 1988; Gipson and Hubert 1993). When filled to capacity, the reservoir has a surface area of 17,000 ha and a surface elevation of 1,841 m above sea level, is 145 km long, and has a maximum depth of 134 m (Schneidervin and Hubert 1987). Surface water temperatures often exceed 20°C during the summer, but temperatures are approximately 5°C at depths of ≥ 30 m. FGR has three primary inputs: Green, Blacks Fork, and Henrys Fork rivers. The Green River contributes ~80% of the water volume to the reservoir, the Blacks Fork and Henrys Fork rivers contribute ~15% combined, and the remaining volume comes from various small tributaries (Madison and Waddell 1973). The outflow of FGR is the Green River and is the largest tributary to the Colorado River (Gray et al. 2011). Dissolved solids in the reservoir primarily originate from the Green River (~60% of the total dissolved solids), followed by the Blacks Fork and Henrys Fork rivers (~20% combined) and various small tributaries (Madison and Waddell 1973).

The Green River basin extends approximately 240 km eastward from the Wyoming Mountains to the Rawlins uplift, with the Gros Ventre Mountains, Wind River Mountains, and Granite Mountains to the north and Uinta Mountains to the south (Surdam and Wolfbauer 1975). The Green River originates in the Wind River Mountains, whereas the Blacks Fork River and Henrys Fork River originate in the Uinta Mountains. The Green River Formation was formed from the playa-lake complex of ancient "Lake Gosiute" during the Eocene Epoch. A combination of Precambrian granite along with Paleozoic and Mesozoic sedimentary rocks is exposed in the drainage basin. The Unita Mountains are classified as a thick siliciclastic succession formed during the Neoproterozoic Era dominated by cross-bedded quartzite and sandstone, siltstone, and shale (Dehler et al. 2010).

FGR is typically divided into three regions (Inflow, Open Hills, and Canyon Regions) for management and research purposes based on bathymetric, limnological, and biological characteristics (Figure 1; Stone and Eiserman 1979; Haddix and Budy 2005; Mosley et al.

2008). FGR is comanaged by WGFD and Utah Division of Wildlife Resources. Sport fishes in the reservoir include Lake Trout, Smallmouth Bass *Micropterus dolomieu*, Rainbow Trout *Oncorhynchus mykiss*, Brown Trout *Salmo trutta*, Bonneville Cutthroat Trout *O. clarkia utah*, and kokanee (Haddix and Budy 2005; Mosley et al. 2008). Although not considered a sport fish, Burbot *Lota lota* has increased in abundance in FGR since its initial detection in the early 2000s, with unknown effects to sport fishes (Gardunio et al. 2011). Following completion of the dam, management initially focused on Rainbow Trout, which declined in abundance as Utah Chub became established (Stone and Eiserman 1979). Kokanee were introduced to FGR in 1963 to compete with Utah Chub (Stone and Eiserman 1979; Teuscher and Luecke 1996). Kokanee source populations included fish from Granby Reservoir, Colorado (Canning 1996), and a commercial stock from Washington (Modde 1992). Brown Trout and Smallmouth Bass were introduced in 1967 to reduce Utah Chub abundance through piscivory. Lake Trout immigrated to the reservoir in the early 1970s from an upstream reservoir and fed almost extensively on Utah Chub (Yule 1992; Yule and Luecke 1993; Teuscher and Luecke 1996). Although kokanee were initially stocked to compete with Utah Chub and later stocked to serve as an additional prey resource for Lake Trout, they are also a popular sport fish (Gipson and Hubert 1993). For the last decade, anglers targeted kokanee the most out of all fish in FGR (Mosley et al. 2013).

Water sampling

We collected water samples during June and July 2020 from the reservoir, major tributaries, known spawning tributaries, and hatcheries that produced kokanee for FGR. We collected water samples at the surface and at depths from five random locations in the Inflow, Open Hills, and Canyon regions of the reservoir. We also collected samples at the confluence of the Blacks Fork and Green rivers, the inflow of spawning tributaries (i.e., Sheep Creek and Henrys Fork River), and near Flaming Gorge Dam. We collected these additional samples at the surface and at depths to identify variation in chemical composition where the tributaries mix with the main body of the reservoir (Figure 1; Madison and Waddell 1973). We took samples at depths in the reservoir averaging 15.7 m and collected them using a Kemmerer bottle (Wetzel and Likens 2000). Additionally, we collected water samples from tributaries near the mouth, approximately midway from the mouth to the nearest upstream barrier, and just downstream of the nearest upstream barrier. Barriers that blocked fish movement included dams (e.g., diversion dams) and natural barriers (e.g., waterfalls). We sampled the Henrys Fork River only at the mouth and at the nearest barrier due to access limitations. We sampled tributaries at base flow in July (Kennedy et al. 2000). Due to the short period of time that kokanee are present in spawning tributaries, we

could not identify a clear chemical signature representing the tributary (Kennedy et al. 1997). We did not include water chemistry results from tributaries in further analyses. We collected two water samples from each hatchery, one sample at the water source before entering the hatchery and an additional sample from holding tanks where fish were reared. Overall, we collected 38 water samples from the reservoir, 11 from tributaries, and 24 from hatcheries (Table S1, *Supplemental Material*).

Before sample collection, we washed 50-mL polypropylene vials, lids, and 10 mL-polypropylene syringes using a 6 N hydrochloric acid bath for 2 h, followed by three rinses with ultrapure water and a 1% trace-metal-grade nitric acid bath for 24 h (Kennedy et al. 2000; Barnett-Johnson et al. 2008; Heckel et al. 2020). We then rinsed the vials, lids, and syringes three times with ultrapure water (18.20 MΩ$^+$ cm) and let them air dry, and we stored all materials in sterile Whirl Paks (Nasco, Fort Atkinson, WI). We filtered all water samples through 25-mm-diameter, 2-µm syringe filters (GE, Pittsburgh, PA). Personnel at the University of California, Davis, prepared water samples for microchemistry analysis by first dissolving the sample and purifying it through a specific ion-exchange resin, strontium resin (Eichrom Technologies, Inc., Lisle, IL), in a class 100 clean laboratory facility. The personnel then reconstituted the samples in ultrapure subboiling double-distilled 2% nitric acid and analyzed the samples for strontium isotopes (^{87}Sr/^{86}Sr). We identified strontium isotopes using inductively coupled plasma mass spectrometry using a Nu Plasma HR (Nu032; North Wales, UK) multiple-collection, high-resolution, double-focusing plasma mass spectrometer system at the University of California, Davis. We used replicate analyses of the National Institute of Standards and Technology standard reference material (SRM-987) to evaluate performance of analytical methods and to estimate error (McArthur et al. 2001).

Fish sampling

We initiated otolith collection in the summer of 2018 and continued through 2020. We used midwater curtain nets, trawls, creel surveys, sinking gill nets, and weirs to sample kokanee in FGR and its tributaries. We used midwater curtain nets (i.e., suspended monofilament gill nets) to capture age 1 and older kokanee in the reservoir. We used trawls to capture age 0 and older kokanee in the reservoir and creel surveys to sample angler-harvested fish. We used sinking gill nets to capture shoreline-spawning kokanee and weirs to capture tributary-spawning kokanee. We collected fish during the late spring and early summer of 2020 from hatcheries that produce kokanee for FGR.

Midwater curtain nets were 61 m long and consisted of eight, 7.6-m-long panels with various mesh (1.90-, 2.54-, 3.17-, 3.81-, 4.44-, 5.08-, 5.71-, or 6.35-cm bar-measure mesh). We set midwater curtain nets in each region of the reservoir at various depths from mid-June

to mid-July. We placed nets from 2018 to 2020 at long-term monitoring sites used by WGFD. In 2020, we selected additional net locations using a stratified random sample; strata were regions of FGR (i.e., Inflow, Open Hills, and Canyon). We set nets for 15 net nights in 2018, 20 net nights in 2019, and 36 net nights in 2020. Utah Division of Wildlife Resources conducted trawl surveys in August 2020 using a midwater collapsible trawl in each region of the reservoir. We did not include data from trawl surveys in the analysis because they sampled few kokanee ($n < 20$). We conducted creel surveys between mid-June and early July. Regardless of where creel surveys occurred, we assigned fish to the region of the reservoir where anglers harvested them. We targeted shoreline-spawning aggregations in each region of the reservoir with short-duration sinking gill nets from September to October (48.7 m long, 1.8 m deep, and 2.54-cm bar-measure mesh). We did not sample shoreline-spawning kokanee in the Canyon Region in 2019 due to a missed spawning event. We captured tributary-spawning kokanee using weirs in the Henrys Fork River and Sheep Creek in late September and mid-October. We sampled fish from weirs after WGFD hatchery personnel collected gametes. We did not sample tributary-spawning kokanee from the Henrys Fork River in 2020. We collected fish from each hatchery before stocking events in the spring and early summer of 2020. Not all hatcheries were producing kokanee when we sampled fish for microchemistry analysis. As such, we used Rainbow Trout as surrogates (e.g., Boulder, Clarks Fork, Saratoga, and Wigwam hatcheries).

We measured kokanee to the nearest millimeter (mid-eye-to-fork length) and removed the sagittal otoliths. We stored otoliths in a coin envelope and allowed them to air dry. We prepared otoliths at the University of Idaho and conducted isotopic analysis at the University of California, Davis, Interdisciplinary Center for Plasma Mass Spectrometry.

Otolith processing

Using a stratified random sample design, we selected up to five fish per 10-mm length category per region of the reservoir per sampling method. We mounted one otolith per fish sulcus acusticus-side down on a microscope slide using Crystalbond 509-3 (Aremco, Valley Cottage, NY). We used a Buehler MetaServ 250 (Buehler, Lake Bluff, IL) grinder–polisher with 600- to 1,200-grit sandpaper and ultrapure water to sand otoliths (Thorrold et al. 1998; Hobbs et al. 2010; Chase et al. 2015; Heckel et al. 2020). We sanded otoliths until the distal side of the otolith was flat. We then flipped the otolith over (i.e., sulcus acusticus-side up) and sanded until the primordium and daily growth rings were clearly visible using a compound microscope. We mounted multiple otoliths for isotopic analysis on petrographic slides using Crystalbond for laser ablation multicollector inductively coupled plasma mass spectrometry (Barnett-Johnson et al. 2008).

We analyzed otoliths using laser ablation multicollector inductively coupled plasma mass spectrometry at the University of California, Davis, Interdisciplinary Center for Plasma Mass Spectrometry. A New Wave Research UP213 (New Wave Research, Fremont, CA) laser ablation system was coupled with a NU Plasma multiple-collection, high-resolution, double-focusing plasma mass spectrometer. We used line scans to measure the strontium isotope ratio (i.e., $^{87}Sr/^{86}Sr$). We initiated line scans approximately 100 μm on the dorsal side of the primordium and traveled through the primordium to the ventral edge. Settings for the line scans included a scanning speed of 5 μm/s, beam width of 40 μm, laser pulse frequency of 10 Hz, and 5- to 15-J/cm² photon output. We normalized values for the $^{87}Sr/^{86}Sr$ isotopic ratio for instrumental mass discrimination by monitoring the $^{86}Sr/^{88}Sr$ isotope ratio (assumed $^{86}Sr/^{88}Sr = 0.1194$). We corrected the interference of rubidium (^{87}Rb) on the $^{87}Sr/^{86}Sr$ isotope ratio by monitoring the ^{85}Rb signal. We evaluated instrumental accuracy and precision by analyzing a White Seabass *Atractoscion nobilis* otolith (mean $^{87}Sr/^{86}Sr$ = 0.70918, SD = 0.0002, $n = 436$) and South China Sea Coral (mean $^{87}Sr/^{86}Sr$ = 0.70927, SD = 0.0003, $n = 134$) compared with the modern seawater value of $^{87}Sr/^{86}Sr$ (0.70918; McArthur et al. 2001).

Krypton is an ever-present spectral interference when measuring strontium isotope values because of its similar atomic mass (Paton et al. 2007). When background krypton is not stable during the initial baseline measurements, it can cause oversubtraction of krypton, thereby altering the $^{87}Sr/^{86}Sr$ value. In addition, when krypton transmission changes during the ablation of the unknown sample, this drift can also affect krypton corrections and the resulting $^{87}Sr/^{86}Sr$ value. We conducted microchemistry analysis of kokanee otoliths over two separate analytical sessions. During the first session, we did not detect any issues associated with krypton interference. However, interference of krypton was an issue during the second analytical session. These issues stemmed from the specialty gas distributor altering their main source of argon (due to COVID-19), leading to five- to tenfold the amount of krypton in the argon supply. To reduce the krypton interference, we plumbed a scrubbed high-purity argon cylinder into the sample carrier gas, reducing the interference to twofold the normal amount. In addition, we constructed a linear model using the ^{83}Kr and $^{87}Sr/^{86}Sr$ values from the otolith edge to externally correct the issues associated with elevated krypton interference during the second analytical session.

After microchemistry analysis, we used the remaining otolith for ageing. We mounted otoliths in epoxy (Koch and Quist 2007) and sectioned them with an IsoMet low-speed saw (Buehler, Lake Bluff, IL) along the dorsoventral plane (Long and Grabowski 2017). We polished sections to improve clarity using 400- to 1,000-grit sandpaper. We aged sections using a dissecting microscope with transmitted light. We measured distance between annuli with Image-Pro Plus software (Media Cybernetics, Rock-

ville, MD) using standard methodologies for annulus identification (Quist et al. 2012; Long and Grabowski 2017).

Data analysis

We reduced and analyzed data from laser ablation multicollector inductively coupled plasma mass spectrometry using the IsoFishR application in R Statistical Software (Willmes et al. 2018; R Core Team 2021). We reduced the data at an integration time of 5 s, blank time of 30 s, minimum ^{88}Sr set to 0.05 V, and maximum ^{88}S set to 9.8 V. We smoothed line scans for visual inspection using a ten-point moving average, and we removed outliers of >2 SD (Chase et al. 2015). We further analyzed the data by manually selecting a sample near the primordium to represent the natal region and a sample near the edge of the otolith to represent the isotopic signature of FGR (Barnett-Johnson et al. 2008; Brennan et al. 2015). We used plots of smoothed data to visually inspect each otolith and identify shifts in isotopic ratios that reflected natal origin. We identified the natal region of suspected hatchery-origin fish by selecting a 200-μm section near the start of the line scan (i.e., near the primordium) between 200 and 600 μm to represent the hatchery where a fish was located just before stocking. Similarly, we identified the natal region of suspected natural-origin kokanee from a 200-μm section selected between 200 and 600 μm. We identified the edge value representing FGR from a 200-μm section that ended between 5 and 100 μm from the end of the line scan. We calculated summary statistics (i.e., mean and SD) of ^{87}Sr/^{86}Sr for the natal and edge region of each otolith.

We conducted normality tests to assess the normality of the ^{87}Sr/^{86}Sr ratio from water samples and otoliths. Assumptions of normality were violated, so we conducted Kruskal–Wallis and post hoc pairwise comparison tests (Dunn test; $\alpha = 0.05$) to compare the ^{87}Sr/^{86}Sr of water samples among regions and depths of FGR (Heckel et al. 2020). We conducted a linear regression to evaluate the relationship between the ^{87}Sr/^{86}Sr of water samples and ratios derived from the edge of otoliths (Bath et al. 2000; Kennedy et al. 2000; Barnett-Johnson et al. 2008; Muhlfeld et al. 2012; Heckel et al. 2020). We conducted Kruskal–Wallis and post hoc pairwise comparison tests (Wilcoxon ranked-sum tests; $\alpha = 0.05$) to compare the ^{87}Sr/^{86}Sr from the otolith edge among hatcheries and FGR (Young 2011; Cuevas et al. 2019). We used the Benjamini–Hochberg adjustment to adjust the type I error rate for all multiple comparisons (Benjamini and Hochberg 1995).

The ^{87}Sr/^{86}Sr signatures from water samples and otolith edge values were correlated but did not follow a 1:1 ratio ($r^2 = 0.78$; Figure 2). As such, we used the otolith edge values to develop the training data sets for the model-based discriminate function analysis (DFA). We used the Mclust package in R (Fraley and Raftery 2002; Scrucca et al. 2016) to conduct a DFA. We used the DFA to evaluate whether ^{87}Sr/^{86}Sr values from hatchery
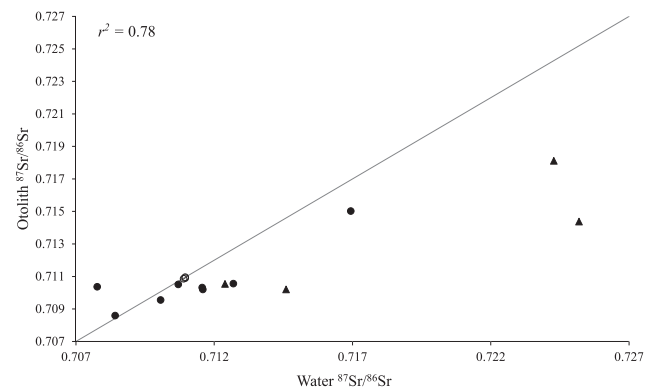

Figure 2. The linear relationship of ^{87}Sr/^{86}Sr ratios in water to otolith edge samples from kokanee *Oncorhynchus nerka* and Rainbow Trout *Oncorhynchus mykiss* collected from 12 hatcheries in 2020. The solid line represents a 1:1 relationship between water and otolith values. Solid circles represent hatcheries that we collected kokanee from, black triangles represent hatcheries that we collected Rainbow Trout from, and open circles represent the regions of Flaming Gorge Reservoir (i.e., Inflow, Open Hills, and Canyon) based on bathymetric, limnological, and biological characteristics.

otoliths and FGR could be used to infer natal origin of unknown kokanee caught in FGR. We averaged values of ^{87}Sr/^{86}Sr from a 200-μm section of the otolith edge from known hatchery-origin fish ($n = 60$) and randomly selected kokanee from FGR ($n = 20$). We used these fish in the training data set. We tested discriminant function models further using K-folds cross-validation to investigate classification accuracy (Fraley and Raftery 2002; Scrucca et al. 2016).

We used results from the DFA to describe growth of kokanee by natal origin and the mean back-calculated lengths at age (mm) to describe growth of natural and hatchery-produced fish. We estimated back-calculated lengths at age using the Dahl–Lea method, $L_i = L_c(S_i/S_c)$, L where L_i is the back-calculated length of the fish when the ith increment was formed, L_c is the length of the fish at capture, S_i is the radius of the otolith at the ith increment, and S_c is the radius of the otolith at capture (Shoup and Michaletz 2017).

Results

In total, we caught 2,677 kokanee ($n = 831$ for microchemistry analysis) varying from 146 to 510 mm mid-eye-to-fork length (366 ± 54 mm) in the reservoir (Table 2). In spawning tributaries (i.e., Henrys Fork River and Sheep Creek), we caught 446 kokanee ($n = 172$ for microchemistry) that varied from 280 to 482 mm mid-eye-to-fork length (371 ± 35 mm). In total, we analyzed 1,003 kokanee otoliths for strontium isotopes (i.e., ^{87}Sr/^{86}Sr; Table S2, *Supplemental Material*).

Strontium isotope signatures of water samples from FGR varied significantly among regions and by depth (Figure 3; $P \leq 0.01$). Post hoc comparisons identified that the water chemistry from the Canyon Region at depth

Table 2. Locations of where we captured kokanee *Oncorhynchus nerka* in regions of Flaming Gorge Reservoir (i.e., Inflow, Open Hills, and Canyon) and spawning tributaries (i.e., Henrys Fork River and Sheep Creek) from 2018 to 2020. Sample size (*n*) and associated minimum (min), maximum (max), and average mid-eye-to-fork length for each capture method are included.

| Location | Capture method | *n* | Mid-eye-to-fork length (mm) | | |
			Min	Max	Average
Inflow	Suspended gill net	343	146	510	340
	Creel survey	346	260	468	389
	Sinking gill net	269	302	479	393
Open Hills	Suspended gill net	270	175	488	358
	Creel survey	299	224	455	366
	Sinking gill net	324	237	479	392
Canyon	Suspended gill net	296	148	457	334
	Creel survey	330	213	455	343
	Sinking gill net	200	314	482	383
Henrys Fork River	Weir	149	301	447	377
Sheep Creek	Weir	297	280	482	368

was significantly different from the Inflow Region surface sample ($P \leq 0.01$), Open Hills Region surface sample ($P \leq 0.01$), and Open Hills Region at depth ($P \leq 0.01$). We did not identify any significant differences for all other comparisons of water samples among depths and regions. Otolith edge values from hatcheries and FGR ($n = 65$) varied significantly ($\chi^2 = 58.3$, $df = 12$, $P \leq 0.01$; Figure 4). FGR was not significantly different from Wigwam Hatchery ($P = 0.84$) but was significantly different from all other hatcheries ($P \leq 0.01$).

We grouped hatcheries as either having an $^{87}Sr/^{86}Sr$ signature that was significantly ($P \leq 0.01$) higher (i.e., Boulder, Clarks Fork, and Dan Speas hatcheries; hereafter presented as "over") or lower (i.e., Daniel, Dubois, Jones Holes, Midway, Tillet, Saratoga, and Whiterocks hatcheries; hereafter presented as "under") than FGR. Auburn Hatchery had a uniquely low $^{87}Sr/^{86}Sr$ signature and was classified separately. We grouped the Wigwam Hatchery with FGR as "natural" origin given the lack of difference in $^{87}Sr/^{86}Sr$ (Table S3, *Supplemental Material*). We

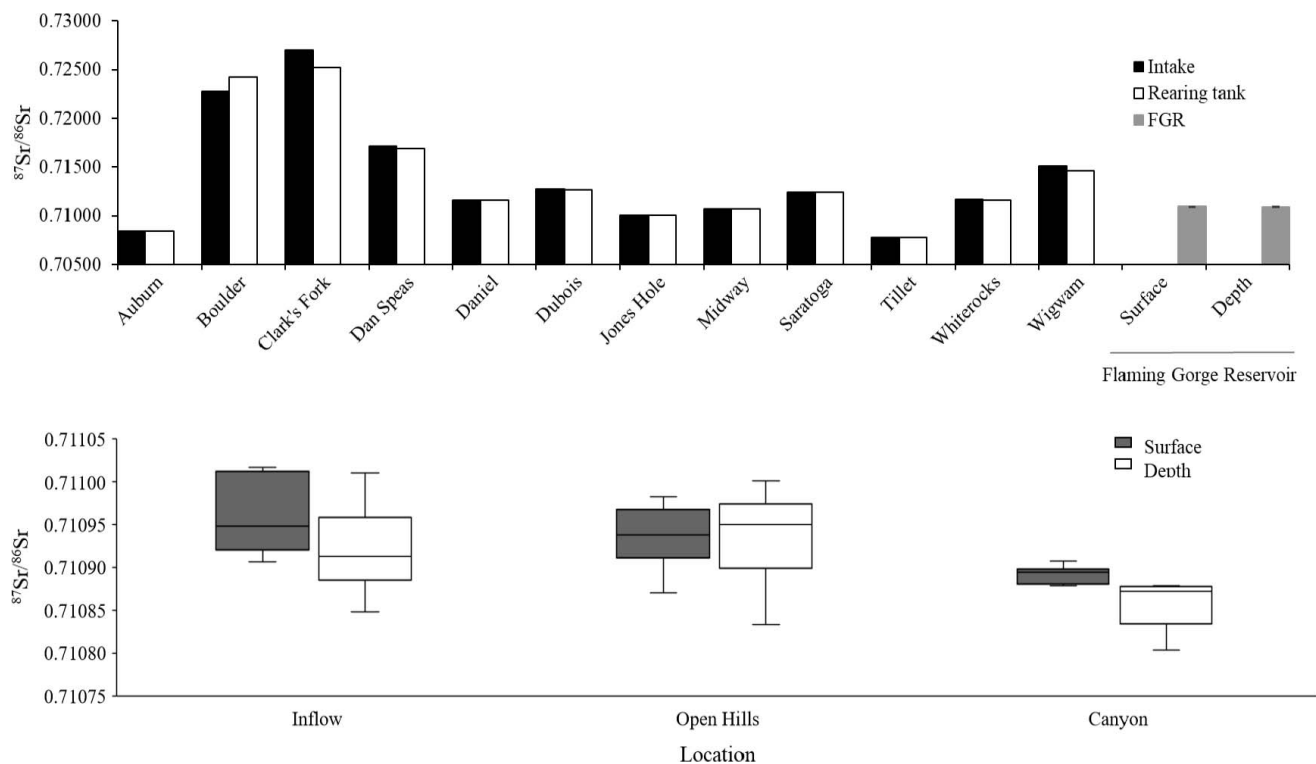**Figure 3.** Strontium isotope ratios (i.e., $^{87}Sr/^{86}Sr$) of water samples collected from hatcheries and Flaming Gorge Reservoir in 2020. The top panel is the $^{87}Sr/^{86}Sr$ from the intake and rearing tanks of each hatchery and the average $^{87}Sr/^{86}Sr$ from surface samples and samples at depth in Flaming Gorge Reservoir. The bottom panel is the difference of $^{87}Sr/^{86}Sr$ of water samples taken on the surface and at depths averaging 15.7 m for each region of Flaming Gorge Reservoir. Regions of the reservoir are based on bathymetric, limnological, and biological characteristics.
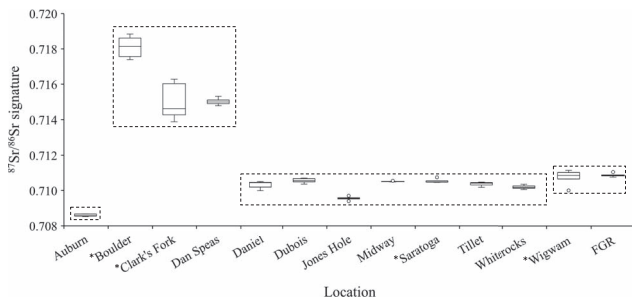
Figure 4. Spatial variability in $^{87}Sr/^{86}Sr$ values from otolith edge values collected from each hatchery in 2020, and random selected otolith edge values from kokanee *Oncorhynchus nerka* captured in Flaming Gorge Reservoir ($n = 65$) from 2018 to 2020. Dashed black boxes represent groupings of hatcheries for model-based discriminate function analysis. Asterisks (*) signify hatchery samples that used Rainbow Trout as surrogates.

combined regions of FGR and classified them as natural origin to reduce classification error.

Similarities in $^{87}Sr/^{86}Sr$ from kokanee in FGR and the Wigwam Hatchery added complexity; however, kokanee from the Wigwam Hatchery were only stocked in FGR in 2016 and 2018, representing 13% of the total kokanee stocked in 2016 and 10% in 2018 (Table 1). We conducted a DFA that included the Wigwam Hatchery in the training data set and a second DFA that excluded the Wigwam Hatchery. Specifically, we completely removed kokanee from the 2016 and 2018 year classes from the analysis of the second DFA. The training data set that included fish from Wigwam Hatchery correctly classified the natal origin of kokanee with 95% accuracy or greater. We classified fish from the Auburn and over groups with 100% accuracy, while we classified the under and natural groups with 95% accuracy. Cross-validation of the training data that included Wigwam Hatchery identified a 5% classification error. The training data set that excluded the Wigwam Hatchery correctly classified natal origin of kokanee with 97% accuracy or greater. We classified the Auburn and over groups with 100% accuracy. We classified fish representing the under and natural groups with 97% accuracy. When cross-validated, we identified a 5% error from the training dataset that excluded Wigwam Hatchery.

Using the DFA that included fish from Wigwam Hatchery, we assigned 1,003 kokanee a natal origin. Kokanee from 2013 to 2019 year classes were represented in the sample, but the 2013 and 2019 year classes had low sample sizes ($n < 15$), and we removed them from further analyses. The contribution of hatchery kokanee varied from 14 to 56% across year classes and was similar regardless of whether we included fish from Wigwam Hatchery in the analysis (Figure 5). We observed the highest percentage of natural-origin kokanee in 2014 and 2017, where they made up over 60% of fish in the system. The contributions of different hatchery groups also varied among years. Auburn fish often composed greater than 50% of the hatchery contributions to the population at large. Hatchery kokanee in the reservoir varied from 21 to 50% of the sample, which was similar
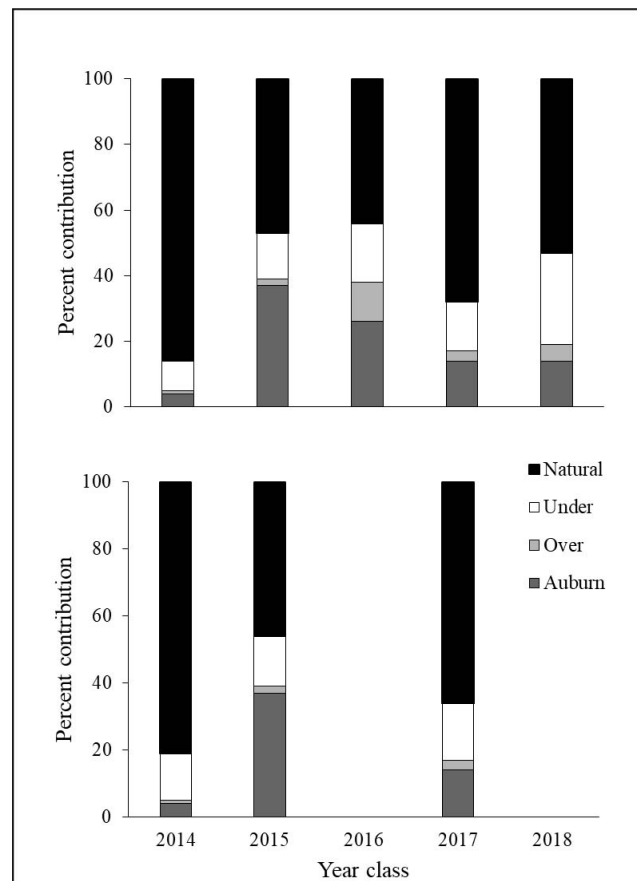

Figure 5. The percentage of kokanee *Oncorhynchus nerka* assigned to natal origin based on $^{87}Sr/^{86}Sr$ signature of all aged fish that we analyzed for microchemistry from 2018 to 2020 by year class. We used a model-based discriminant function analysis to assign fish to natal origin. The top panel is assignment using the discriminant function analysis including the Wigwam Hatchery. The bottom panel is assignment using the discriminant function analysis excluding the Wigwam Hatchery and no assignments to 2016 and 2018 year classes.

to what we observed in the creel (18 to 50%; Figure 6). Notably, natal contributions to the population and creel were similar (differed by <5%) using the alternative DFA that excluded Wigwam Hatchery.

We summarized natal composition of shoreline-spawning ($n = 239$) and tributary-spawning ($n = 172$) aggregates by sample year (Figure 7). Using the DFA that included Wigwam Hatchery, hatchery contributions to shoreline-spawning aggregates varied from 19 to 58%. Tributary-spawning aggregates had higher contributions of hatchery-produced kokanee (40 to 90%) than those on the shoreline. The Auburn and under hatchery groups were present in both spawning aggregations across all sample years, making up over 75% of the hatchery contributions each year. Tributary-spawning aggregates were primarily composed of hatchery-origin fish, except in 2020 when we observed a high percentage of natural-origin fish. The alternate DFA produced slightly different percentages of natal contributions (differences of 0 to 26%), but overall, trends were similar (Figure 7).
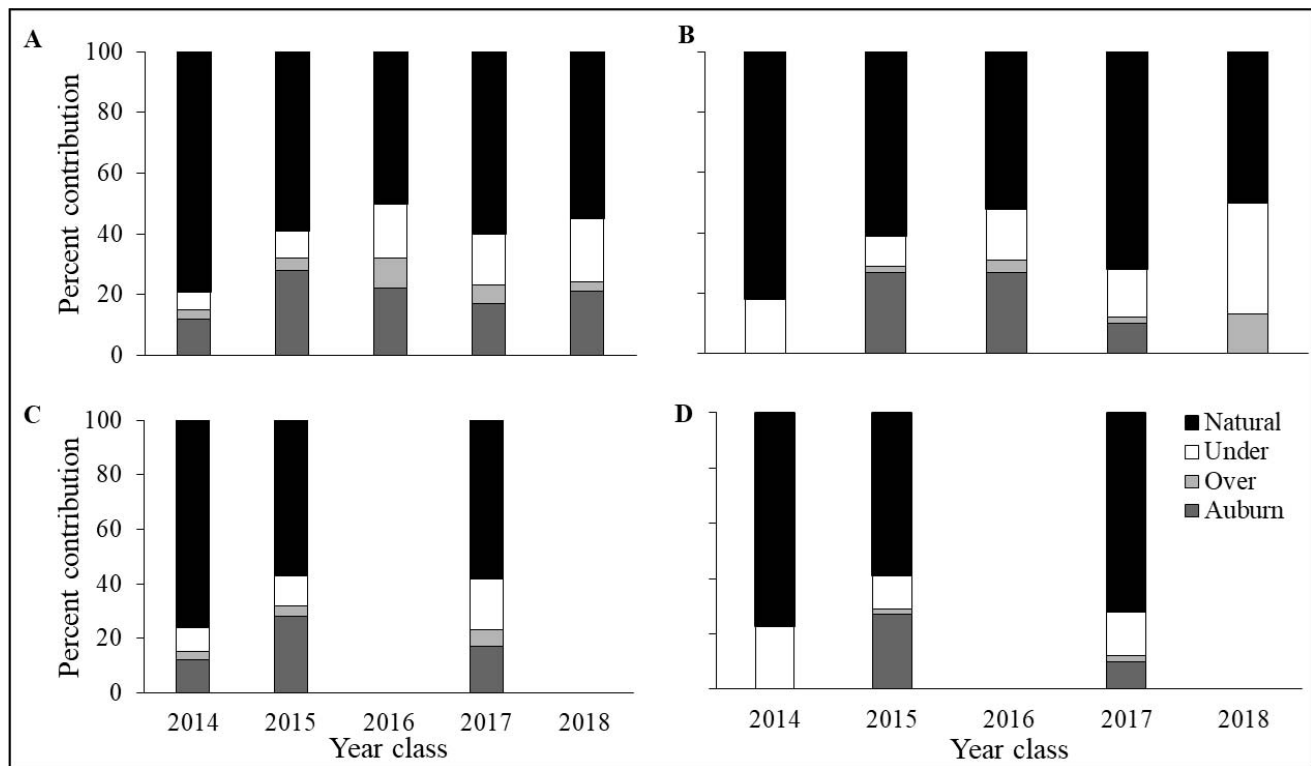
Figure 6. The percentage of kokanee *Oncorhynchus nerka* assigned to natal origin based on $^{87}Sr/^{86}Sr$ signature of fish sampled from 2018 to 2020 using suspended gill nets (**A** and **C**) and creel surveys (**B** and **D**) by year class. We used a model-based discriminant function analysis to assign fish to natal origin. Data in **A** and **B** are assignments using the discriminant function analysis that included the Wigwam Hatchery. Data in **C** and **D** are assignments using the discriminant function analysis that excluded the Wigwam Hatchery and no assignments to 2016 and 2018 year classes.

Patterns in the percentage of fish that were stocked relative to the percentage in the population were variable through time (Figure 8). Initially, "under" hatcheries tended to have fewer fish in the population than would be expected based on what was stocked. We observed the opposite pattern for the Auburn Hatchery, where stocked kokanee appeared to compose a larger portion of the population than would be expected. Contributions of the "over" hatcheries that we observed in the population were similar to what was stocked for all year classes.

Kokanee sampled from FGR varied in age from 1 to 6 years, whereas kokanee sampled from spawning aggregates (i.e., shoreline and tributary) varied from 2 to 4 years. Over 90% of natural-origin kokanee (92%) and 87% of hatchery kokanee were ages 3 and 4 (Table 3). Few fish ($n = 13$) were age 5 or older, only one of which we estimated to originate from a hatchery (Figure 9). Kokanee in FGR exhibited fast growth, reaching 300 mm by age 3 (Table 3). Hatchery-produced kokanee were slightly larger, on average, than natural-origin fish, but differences of the mean back-calculated length-at-age were generally less than 15 mm.

Discussion

Previous studies used otolith microchemistry to identify life history variation and natal origin of anadromous (Kennedy et al. 2000, 2002; Barnett-Johnson et al. 2008; Brennan et al. 2015) and freshwater fishes (Muhlfeld et al. 2012; Heckel et al. 2020). By contrast, few studies used otolith microchemistry to identify the contributions of natural and hatchery-produced fishes in a freshwater system (also see Marklevitz et al. 2016). Identifying contributions of hatchery-produced kokanee to FGR is of particular importance in Wyoming because most of the state's production is allocated to the reservoir. Otolith microchemistry was useful in identifying the natal contributions of the kokanee population in FGR, but additional inferences (e.g., individual hatchery success) were limited using only $^{87}Sr/^{86}Sr$. Understanding natal contributions in the reservoir provides insight that fisheries managers can use to guide management decisions and future investigations on kokanee recruitment in the system.

A variety of biotic and abiotic factors influence natural recruitment and stocking success of kokanee (Vinyard et al. 1982; Sissenwine 1984; Paragamian and Bowles 1995; Modde et al. 1997; Weber and Faush 2003). For example, Paragamian and Bowles (1995) documented that stocking success of kokanee was linked to later stocking dates (e.g., June–August) in Lake Pend Oreille, Idaho. Prey diversity and abundance was higher later in the year, which allowed hatchery-produced kokanee to successfully transition to wild prey items (Rieman and Falter 1981; Vinyard et al. 1982; Paragamian and Bowles 1995).
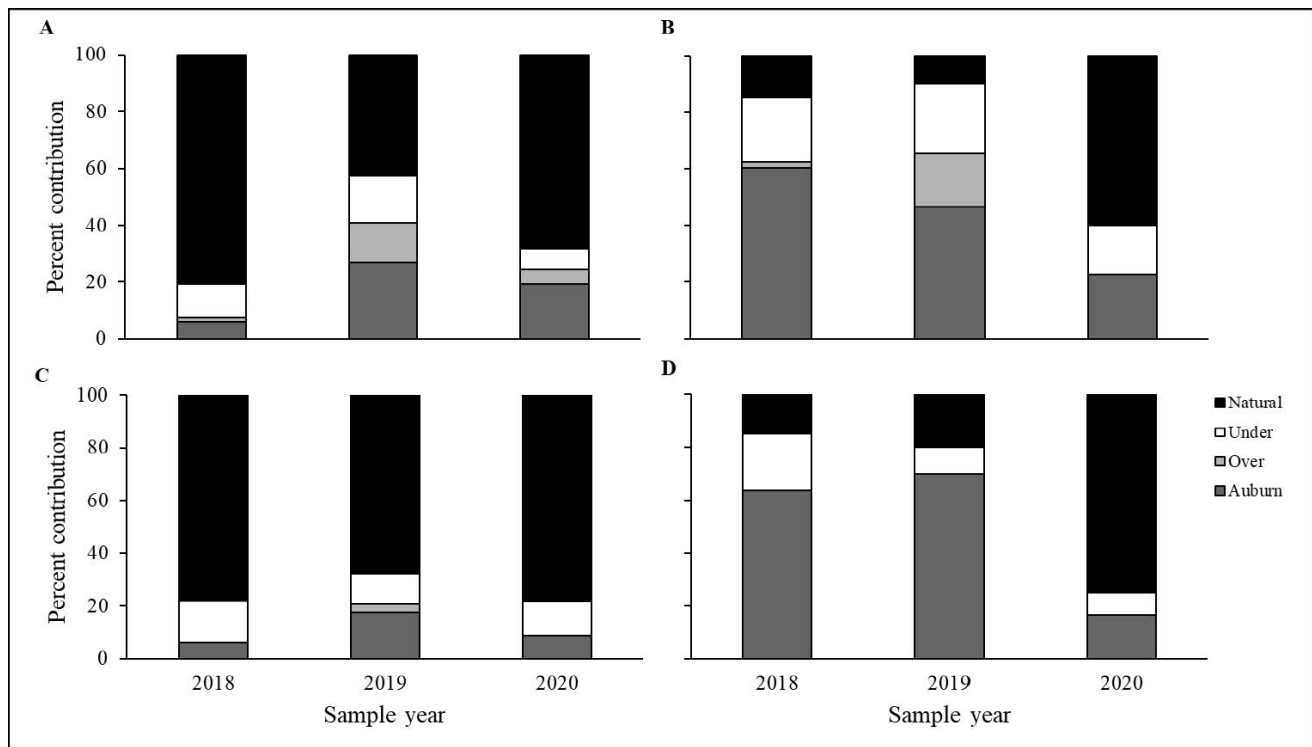
Figure 7. The percentage of kokanee *Oncorhynchus nerka* assigned to natal origin based on ^{87}Sr/^{86}Sr signature of fish sampled from 2018 to 2020 from shoreline-spawning aggregates (**A** and **C**) and tributary-spawning aggregates (**B** and **D**) by sample year. We used model-based discriminant function analysis to assign fish to natal origin. Data in **A** and **B** are estimated origins using the discriminate function analysis that included the Wigwam Hatchery. Data in **C** and **D** are estimated origins using the discriminate function analysis that excluded the Wigwam Hatchery and no assignments to 2016 and 2018 year classes.

Martinez and Wiltzuis (1995) found that water temperature influenced kokanee recruitment in Lake Granby, Colorado. Specifically, warmer water temperatures were associated with increased growth and survival of stocked kokanee. Stocking records for FGR indicated that from 2013 to 2016, a large portion of the kokanee from the under group were stocked at an earlier date than the
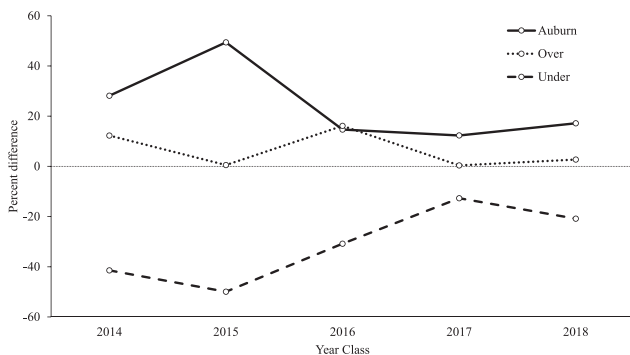

Figure 8. Difference between percentage of hatchery kokanee *Oncorhynchus nerka* stocked and percentage of hatchery kokanee observed from sampling events using natal assignment from discriminate function analysis. These data include kokanee that we sampled in Flaming Gorge Reservoir from 2018 to 2020 using suspended gill nets. Each year class includes all ages, and each line represents a different hatchery group. We grouped hatcheries based on similar ^{87}Sr/^{86}Sr values.

Auburn or over groups. The earlier stocking date may be linked to cooler temperatures and lower prey availability in FGR and may explain why the under group appeared in our sample at lower proportions than expected based on the number of fish stocked. In comparison, the Auburn group was typically stocked at a later date and was overrepresented in our sample for similar year classes. From 2017 to 2020, under-group kokanee were stocked at a time similar to other hatchery groups. During this timeframe, the under group was represented in our sample in similar proportions to their stocking rates. However, many factors (e.g., water temperature and zooplankton abundance) that could be used to help validate recruitment variability and stocking success were not available for FGR during the study period. As such, enhanced monitoring of factors that potentially influence recruitment and stocking success will be necessary to better understand whether alternative stocking strategies are needed.

In a dual-purpose system, identifying how hatchery kokanee are exploited in the system is of utmost importance. In FGR, otolith microchemistry revealed that the natal composition of the creel was similar to the population at large. Additionally, growth of natural and hatchery-produced kokanee suggests that they occupy similar habitats and are equally vulnerable to anglers. In contrast to identifying that hatchery resources return to the recreational creel, understanding their role as a prey resource is useful when used to serve a dual purpose

Table 3. Comparisons of growth using back-calculated lengths-at-age (mm) of natural and hatchery-produced kokanee *Oncorhynchus nerka* that we captured in Flaming Gorge Reservoir and its tributaries from 2018 to 2020. We assigned natal origins of kokanee using the model-based discriminate function analysis that excluded the Wigwam Hatchery. We estimated back-calculated length using the Dahl–Lea method. We estimated mean (mean [SD; *n*]) mid-eye-to-fork length (mm).

Natal origin	Age (years)					
	1	**2**	**3**	**4**	**5**	**6**
Natural	104.3 (22; 319)	211.3 (32; 319)	303.1 (30; 303)	372.1 (25; 180)	423.6 (14; 9)	480.6 (9; 3)
Hatchery	111.7 (21; 199)	225.8 (36; 196)	316.3 (35; 173)	373.4 (29; 75)	429.0 (—; 1)	—

(Wydoski and Bennett 1981). In many systems where Lake Trout abundance has increased, kokanee abundance has declined due to increased predation (Martinez and Wiltzius 1995; Hansen et al. 2010; Schoen et al. 2012; Pate et al. 2014). For example, Schoen et al. (2012) identified that declines of kokanee abundance in Lake Chelan, Washington, were a result of increased Lake Trout predation. Similarly, Lake Trout predation significantly reduced kokanee abundance in Lake Pend Oreille (Hansen et al. 2010). Yule and Luecke (1993) identified that Lake Trout prey on kokanee in FGR, but piscivory is typically limited to Lake Trout greater than 600 mm. In addition, Yule and Luecke (1993) suggested that juvenile Lake Trout in FGR have limited access to small prey fish due to minimal spatial and temporal overlap. Although vulnerability to anglers may be similar between natal origins, the effects of Lake Trout predation on kokanee origin are still unknown. The current stocking strategies

and interactions between kokanee and Lake Trout support a popular kokanee fishery as well as a trophy Lake Trout fishery in FGR. Although it was not a focus of this research, distinguishing predation rates between natal origins could be used to guide stocking strategies that balance predation rates and returns to the recreational creel to meet management objectives. Future investigations focused on predation rates may be warranted if kokanee or Lake Trout abundance changes in the reservoir.

Understanding the natal composition of spawning aggregates can help guide stocking strategies that lead to a heterogenous population that is resilient to environmental changes (Burger et al. 2000; Carlson et al. 2016). However, due to data constraints and the limited information of spawning aggregates in the system, factors influencing the composition of spawning aggregations in FGR are unknown. Otolith microchem-
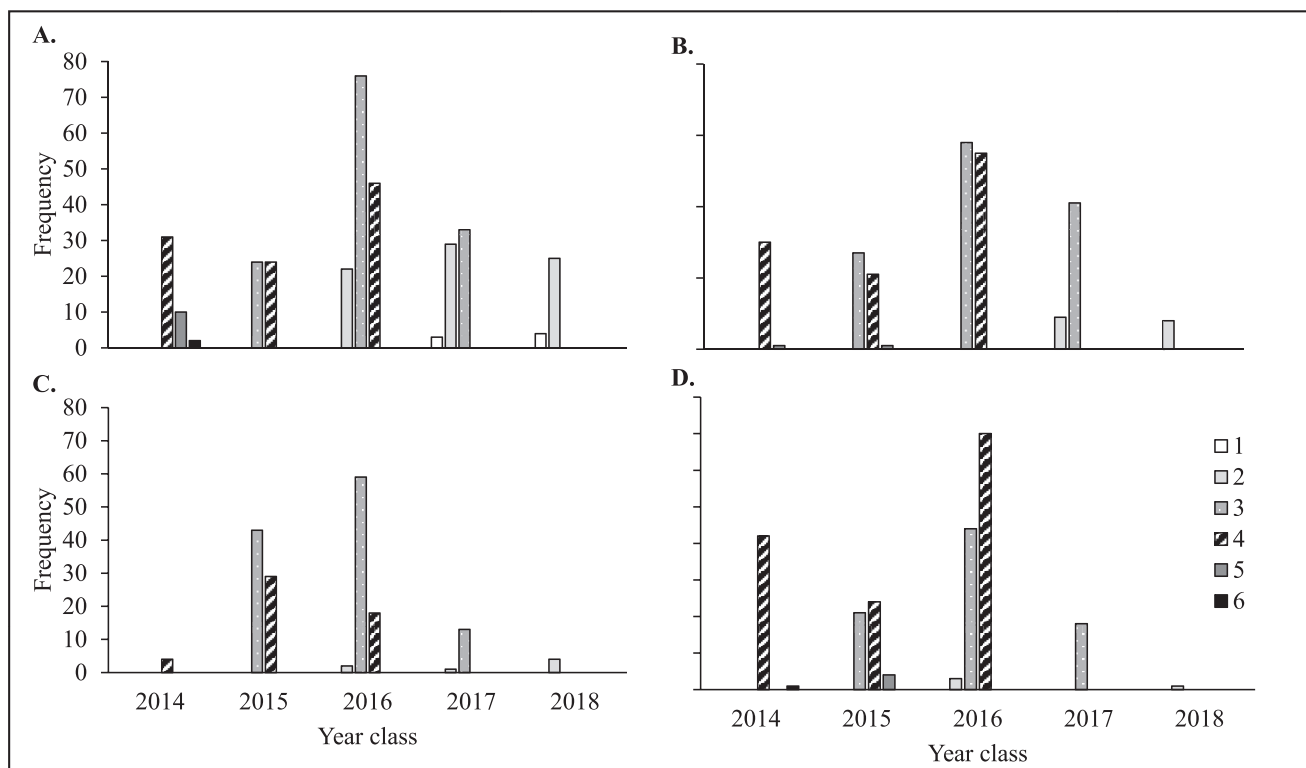

Figure 9. Age-frequency distribution of kokanee *Oncorhynchus nerka* by year class sampled in Flaming Gorge Reservoir from 2018 to 2020. Each panel represents the age-frequency by sampling method, and ages are distinguished by different bar patterns. Data in **A** represent suspended gill nets, data in **B** represent the recreational creel survey, data in **C** represent tributary-spawning kokanee sampled with weirs, and data in **D** represent shoreline-spawning kokanee sampled with sinking gill nets.

istry analysis identified that shoreline-spawning aggregates in FGR contained higher percentages of natural fish, whereas tributary-spawning aggregates were dominated by hatchery kokanee in most years. Averett and Espinosa (1968) reported similar findings in Odell Lake, Oregon, and used marked kokanee to identify that shoreline-spawning aggregates of kokanee mostly consisted of natural-origin fish, whereas tributary-spawning aggregates were predominately hatchery fish. In addition, movement of hatchery fish along the shoreline before spawning suggested that kokanee were searching for suitable spawning locations due to the lack of natal sites in the lake (Averett and Espinosa 1968). In 2020, the reduced contributions of hatchery kokanee in tributaries to FGR compared with previous years may be due to the weak year class of hatchery fish in 2017. Although the different spawning aggregates were typically dominated by either natural or hatchery-origin kokanee, kokanee from both natal origins were present in both spawning aggregates across all sample years. Whether recruitment of natural-origin kokanee results from shoreline or tributary-spawning aggregates is unknown. Otolith microchemistry analysis focusing only on the ^{87}Sr/^{86}Sr ratio was not enough to identify individual hatcheries, specific tributaries, or specific regions in FGR. The use of additional isotopic and/or elemental ratios may help to identify more specific natal origins that can be used to better understand the composition of spawning aggregates and identify areas that may need protection or enhancement to promote spawning. Similarly, traditional methods (e.g., marking and tagging) or new developing methods (e.g., parentage-based tagging) to evaluate stocking strategies may be necessary if concerns related to spawning aggregations arise.

Otolith microchemistry can be a powerful tool to reconstruct the life history and natal origins of fishes (Barnett-Johnson et al. 2008; Muhlfeld et al. 2012; Brennan et al. 2015; Heckel et al. 2020) but does not come without challenges. During our study, we identified that many of the water samples and otoliths collected from hatcheries did not have the same chemical composition. Although not completely understood, the difference between hatchery water and otoliths may be due to the chemical composition of fish feed that can differ from hatchery water (Kennedy et al. 2000; Barnett-Johnson et al. 2008). Additional challenges using otolith microchemistry included identifying the chemical composition of hatchery sources that infrequently stock kokanee. Several hatcheries did not produce kokanee at the time of this study but had previously stocked kokanee into FGR. As such, we used Rainbow Trout in place of kokanee to represent those hatcheries. Although the chemical composition of different species occupying the same watershed may be correlated, they may not follow a strict 1:1 ratio (Prichard et al. 2018). However, hatcheries that were represented by Rainbow Trout rarely stock kokanee into the reservoir, and their contributions only accounted for 2 to 18% of the annual production from 2014 to 2019. The removal of all fish from the 2016 and 2018 year classes in the alternative DFA reduced the number of

hatcheries represented by Rainbow Trout to only two hatcheries. Kokanee from those two hatcheries only accounted for 2 to 7% of the total number of fish stocked. Additionally, we grouped the two remaining hatcheries (Boulder and Clarks Fork) together, and both otolith and water samples displayed ^{87}Sr/^{86}Sr values dissimilar to FGR. As such, fish from these hatcheries likely assigned to the correct natal origin. If the kokanee population continues to be monitored using otolith microchemistry, identifying the chemical composition of otoliths from hatcheries that infrequently stock kokanee would be advantageous.

Growth of wild and hatchery fishes is highly variable across species and systems (Dwyer and Piper 1984; Hoffman and Bettoli 2005; Meyer et al. 2012; Zorn 2015). Observed differences (or similarities) of growth between natural and hatchery-produced fish may be influenced by behaviors that are learned and/or artificially selected for in the hatchery system (Dwyer and Piper 1984; Metcalfe et al. 2003; Peery and Bjornn 2004). Hatchery-produced fish may also perform differently based on the characteristics of receiving waters, such as available prey and water temperature (Martinez and Wiltzuis 1995; Paragamian and Bowles 1995). Although we did not evaluate factors influencing growth, we identified that growth of natural and hatchery-produced kokanee was similar in FGR. Kokanee in FGR are reared from broodstock captured in natural systems and stocked as fingerlings. The source of broodstock coupled with a limited time in the hatchery may contribute to similarities in growth between natural and hatchery-produced kokanee in the system. In addition to similar growth between natural and hatchery-origin kokanee, it is worth noting that kokanee grew relatively fast in FGR compared with kokanee in other systems (Markevich 2008; Branigan et al. 2019). Markevich (2008) reported that the fork length of age 3 kokanee captured from Kronotskoe Lake, Russia, averaged about 190 mm. Additionally, age 3 kokanee sampled from Lake Pend Oreille and Mirror Lake, Idaho, displayed total lengths of less than 300 mm (Branigan et al. 2019). For comparison, natural and hatchery-origin kokanee in FGR were greater than 300 mm in mid-eye-to-fork length at age 3. The fast growth of kokanee observed in FGR suggests that biotic and abiotic conditions that promote fast growth are available to kokanee regardless of natal origin. Similarly, the fast growth observed for both natal origins may diminish any advantages one natal origin may have over another. Investigations identifying conditions in the hatchery and/or factors of FGR that influence growth may be necessary if changes in growth of kokanee are observed.

Here, we provide information regarding the contributions of natal origin to multiple aspects of the kokanee fishery in FGR with high confidence. Previous otolith microchemistry studies reported similar assignment rates and cross-validation results, but multiple isotopic and/or elemental ratios were typically analyzed (Veinott and Porter 2005; Longmore et al. 2010). We focused on the overall contributions of natal origins rather than contributions from specific hatcheries, and the high assign-

ment rates observed were likely an artifact of grouping multiple hatcheries together. The use of additional isotopic ratios or the combination of additional isotopic ratio and elemental ratios may be helpful in isolating individual hatcheries in the future (Moreira et al. 2018). Under current stocking strategies, hatchery-produced kokanee contribute to the population at large, the creel, and various spawning aggregations. It is currently unknown if hatchery contributions suppress natural recruitment, and additional information is needed before major changes to stocking strategies are implemented. Further investigations focused on factors contributing to stocking success and natural recruitment (e.g., predation and prey density) would be particularly useful. Additionally, the implementation of a tagging or marking program (e.g., thermal marking) would increase the ability of WGFD and Utah Division of Wildlife Resources to regularly monitor the kokanee population; however, if otolith microchemistry is used, additional isotopic ratios and elemental ratios would be useful. Furthermore, a marking program would allow more precise evaluation of stocking strategies from individual hatcheries and the associated environmental conditions at the time of stocking if a single hatchery has multiple stocking events throughout the year. Although this research was focused on FGR, this study showcases how otolith microchemistry analyses can contribute broadly to our understanding of the ecology of kokanee in reservoir systems.

Supplemental Material

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Table S1. Location of water samples collected for strontium isotope (i.e., $^{87}Sr/^{86}Sr$) analysis in 2020 including the region (hatchery, Flaming Gorge Reservoir region, or tributary), locality within a region (surface or depth; inflow or holding tank), Universal Transverse Mercator coordinate, and the $^{87}Sr/^{86}Sr$ value.

Available: https://doi.org/10.3996/JFWM-22-009.S1 (265 KB DOCX)

Table S2. Sample year, Flaming Gorge Reservoir region, sample method, and $^{87}Sr/^{86}Sr$ ratio mean and standard deviation from the natal region of the otolith from individual kokanee *Oncorhynchus nerka* that we sampled in FGR from 2018 to 2020. Age-at-capture, mid-eye-to-fork length at capture, and classification from model-based discriminate function analysis are also included. Classifications are from the discriminate function analysis that included the Wigwam Hatchery and the discriminate function analysis that excluded the Wigwam Hatchery with no natal assignment to the 2016 and 2018 year classes.

Available: https://doi.org/10.3996/JFWM-22-009.S1 (265 KB DOCX)

Table S3. Sample year, hatchery sampled, and mean and standard deviation of the $^{87}Sr/^{86}Sr$ ratio of otoliths from hatchery-sampled kokanee *Oncorhynchus nerka* in 2020. Hatcheries sampled were located in Wyoming and Utah. Bold headings indicate hatchery groupings that we used in the model-based discriminate function analysis. Agencies include Wyoming Game and Fish Department, Utah Division of Wildlife Resources, and U.S. Fish and Wildlife Service. Hatchery samples that used Rainbow Trout as surrogates are represented by asterisks (*).

Available: https://doi.org/10.3996/JFWM-22-009.S1 (265 KB DOCX)

Reference S1. Madison RJ, Waddell KM. 1973. Chemical quality of surface water in the Flaming Gorge Reservoir area, Wyoming and Utah. U.S. Geological Survey Water-Supply Paper 2009-C. Washington, D.C.: U.S. Government Printing Office.

Available: https://doi.org/10.3996/JFWM-22-009.S2 (520 KB PDF)

Reference S2. Mosley R, Hendrick T, Amadio C, Kieth R. 2013. 2013 Flaming Gorge Reservoir creel survey. Salt Lake City: Utah Department of Natural Resources, Division of Wildlife Resources.

Available: https://doi.org/10.3996/JFWM-22-009.S3 (847 KB PDF)

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