

ARTICLE

# Combining Genetic, Isotopic, and Field Data to Better Describe the Influence of Dams and Diversions on Burbot Movement in the Wind River Drainage, Wyoming

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**Abstract**

Dams and water diversions fragment habitat, entrain fish, and alter fish movement. Many Burbot *Lota lota* populations are declining, with dams and water diversions thought to be a major threat. We used multiple methods to identify Burbot movement patterns and assess entrainment into an irrigation system in the Wind River, Wyoming. We assessed seasonal movement of Burbot with a mark–recapture (PIT tagging) study, natal origins of entrained fish with otolith microchemistry, and historic movement with genotyping by sequencing. We found limited evidence of entrainment in irrigation waters across all approaches. The mark–recapture study indicated that out-migration from potential source populations could be influenced by flow regime but was generally low. Otolith and genomic results suggested the presence of a self-sustaining population within the irrigation network. We conclude that emigration from natural tributary populations is not the current source of the majority of Burbot found in irrigation waters. Instead, reservoir and irrigation canal construction has created novel habitat in which Burbot have established a population. Using a multi-scale approach increased our inferential abilities and mechanistic understanding of movement patterns between natural and managed systems.

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Freshwater fishes must move between heterogeneous habitats to fulfill spawning and feeding requirements (Schlosser 1991; Schlosser and Angermeier 1995). These movements can cover large distances (Reynolds 1983;

Breaser et al. 1988; Lucas and Batley 1996; Lucas and Baras 2008). Understanding fish movement patterns and the effects of anthropogenic disturbance on movement is important for fish species conservation (Fausch et al.

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2002; Albanese et al. 2004). The construction and use of dams and diversion structures constitute a major threat to aquatic ecosystems that can substantially alter fish movement (Dynesius and Nilsson 1994). Dams and water diversion structures can fragment habitat, block or alter fish movements, and entrap or entrain fish in diverted water, compromising connectivity and movement of individuals between populations (Nerass and Spruell 2001; King and O'Connor 2007; Pelicice et al. 2015).

Large dams are known to lead to large-scale declines in anadromous salmon reproduction due to blocked spawning migration routes (Kareiva et al. 2000). However, it is increasingly evident that small structures and water diversions can have population consequences for many fish species (Poff and Zimmerman 2010; Walters et al. 2014). Even small instream structures can limit the migrations of juvenile fish or of species that are small or weak swimmers (Ficke and Myrick 2009; Gardunio 2014). Likewise, juvenile fish and weak swimmers are unable to avoid high flow velocities associated with reservoir outlets and water diversion inlets, which often leads to high rates of loss from reservoirs and entrainment into diverted water (Grimaldo et al. 2009). Variations in anthropogenic factors (e.g., diverted water volume) and natural factors (e.g., fish proximity to outlet structures due to lake stratification or seasonal migrations in rivers) can result in highly variable losses over time, which can make identification of the extent of these issues a challenge using short-term sampling methods (Walburg 1971; Walters et al. 2012).

Burbot *Lota lota* are highly susceptible to the effects of dams and water diversions (Paragamian et al. 2005; Hubert et al. 2008). The construction of dams is one of the main reasons cited for declines of Burbot (Stapanian et al. 2010). Burbot are weak swimmers and poor jumpers and have a passive larval drift phase, making them unable to cope with both high flow releases and small anthropogenic barriers, such as culverts and diversion dams (Stapanian et al. 2010; Gardunio 2014). As a result, in systems with dams, water diversions, and other barriers, Burbot spawning migrations can be blocked, and entrainment of Burbot into diverted water could result in high rates of mortality and significant population reductions.

The Wind River drainage, Wyoming, contains the southwestern-most North American native population of Burbot. The Burbot is the native apex predator in many of the region's waters, is a popular sport and food fish, and is culturally significant to the Eastern Shoshone and Northern Arapaho American Indian Tribes. Though the drainage has seen relatively little disturbance, water development (primarily for agricultural irrigation) is suspected to be contributing to Burbot declines (Hubert et al. 2008). During the first three decades of the 20th century, natural lakes on tributaries to the Wind River were augmented with dams, and a large diversion was built on the Wind

River to store and supply irrigation water to the region. Burbot have been found entrained at high densities within some of these irrigation canals. High flow releases from dam-augmented natural lakes are suspected of flushing Burbot out of lakes, making them susceptible to entrainment into the irrigation network (Hubert et al. 2008).

Our research objectives were to (1) evaluate whether fish out-migration from a dam-augmented lake is related to high flow releases from the dam; (2) determine the origin of Burbot entrained in the irrigation network; and (3) compare current movement patterns to historical movement patterns as inferred from genetic population structure. We hypothesized that Burbot entrainment into irrigation waters was linked with Burbot out-migration from the closest dam-augmented lake (Bull Lake) during high flow releases. We expected to see increased seasonal fish movement during high-flow events, and we expected that the natal and genetic origins of fish entrained in the irrigation network would primarily correspond to Bull Lake. We used three complementary approaches that assessed movement at different time scales to address our objectives. We conducted a mark-recapture (PIT tagging) study (Dunnigan and Cameron 2008) to examine how seasonal out-migration from lakes is affected by the flow regime; we examined natal origins of entrained Burbot by using otolith strontium isotope analysis (Thorrold et al. 2001); and we evaluated historic movement using high-resolution genomic data for Burbot throughout the drainage (Fontaine et al. 1997; Dunham and Rieman 1999). Given the paucity of studies that combine all three of these approaches, we compare the financial and material inputs required for each method and discuss the varying insights provided by each approach independently and collectively.

## METHODS

*Study area.*—Burbot are found within the Wind River basin in lakes on tributaries that descend from the Wind River Mountains to the main stem of the Wind River; they are also found in diverted irrigation waters (Figure 1). The tributary lakes were formed by glaciation during the Bull Lake and Pinedale glaciations of the Quaternary Ice Age. Missourian-lineage Burbot most likely colonized these lakes sometime after the recession of the Bull Lake and Pinedale glaciations (21,000 years ago), and stable populations now exist within Torrey, Ring, and Trail lakes on Torrey Creek; Upper Dinwoody and Lower Dinwoody lakes on Dinwoody Creek; and Bull Lake on Bull Lake Creek (Abrahamse 2008; Hubert et al. 2008).

Burbot movements in the basin are limited by a variety of natural and anthropogenic barriers. Burbot are able to move downstream out of tributary lakes and into the Wind River and irrigation waters, but movement upstream into the lakes or out of the irrigation waters is

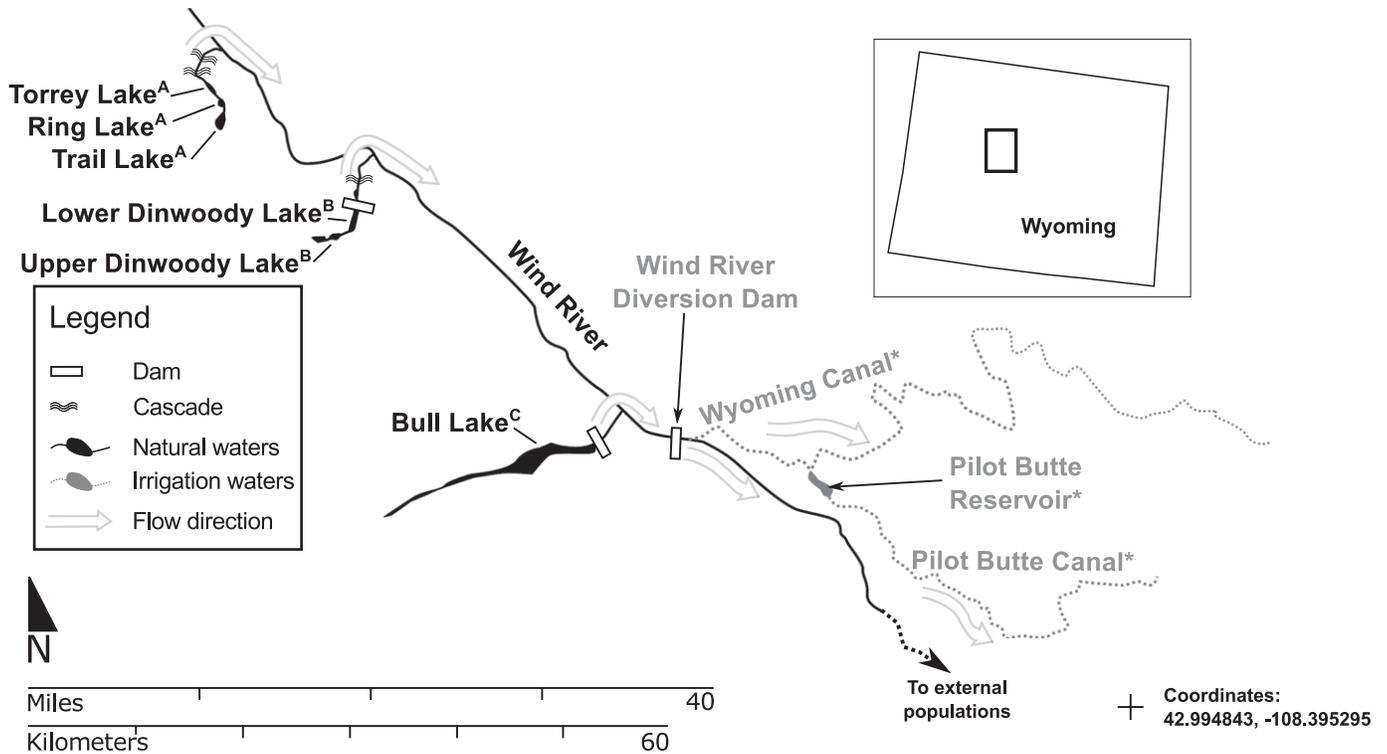


FIGURE 1. Map of water development in the upper Wind River drainage, Wyoming, USA. Asterisks following water body names denote irrigation waters where entrained Burbot have been found; superscript letters indicate potential source population groups of Burbot. The inset figure identifies the location of the Wind River drainage within Wyoming.

highly unlikely due to numerous natural and man-made barriers. Torrey Creek populations are likely isolated from immigration by a step series of cascades below Torrey Lake, but Burbot can move between Torrey, Ring, and Trail lakes (Hubert et al. 2008). There are no complete barriers between Upper Dinwoody and Lower Dinwoody lakes, but these populations are mostly isolated from immigration from the Wind River by a 2-m-high dam (fish can move up through the dam when the gates are fully open) on the outlet of Lower Dinwoody Lake. There are also short, steep river sections, which may have historically prevented Burbot movement into the system (Hubert et al. 2008). Historically, upstream movement in Bull Lake Creek was possible, but Bull Lake Creek was dammed in 1938 to expand Bull Lake, and the dam now acts as a complete barrier to movement into the lake (Hubert et al. 2008). In addition, operations of this dam are believed to negatively affect Burbot recruitment through loss of spawning habitat due to winter draw-downs and forced out-migration of primarily age-0 Burbot during large summer irrigation releases (Bergersen et al. 1993). The outlet is believed to be within habitat and at a depth range used by age-0 Burbot, and the water velocity generated during large releases may be inescapable to these fish.

Burbot can enter the irrigation system via the Wind River Diversion Dam (constructed in 1923), located several miles downstream from the confluence with Bull Lake Creek (Figure 1). From this diversion, the Wyoming Canal transports water to agricultural users as well as to Pilot Butte Reservoir (constructed in 1926). The Pilot Butte Canal transports water from the reservoir to irrigators. At times, Burbot can be found in all three irrigation waters (Pilot Butte Reservoir, Wyoming Canal, and Pilot Butte Canal), but both canals are unused during winter and go dry during that time. Pilot Butte Reservoir holds a moderate Burbot population year-round, but recruitment is thought to be limited due to a lack of deep winter habitat. Burbot are found at high densities ( $>1.3$  Burbot/ $m^3$ ) in Pilot Butte Canal directly below Pilot Butte Reservoir. It was believed that recruitment in all irrigation waters was maintained by immigration from natural waters.

Burbot are scarce in the Wind River itself, with only one having been found during extensive sampling prior to this project (Bergstedt and Bergersen 1992). Therefore, it is thought that the Wind River is primarily a conduit for out-migrants from the tributary populations and that there are few resident Wind River Burbot. The Wind River is braided and flows over mostly small to large gravel and small cobble between the confluences of Torrey and Bull

Lake creeks. Transportation rates of sediment and woody debris are high within the system, resulting in a scarcity of complex habitats suited to Burbot. Several other small entrainment hazards exist on the Wind River and its tributaries, but it is not believed that there are other anthropogenic barriers to upstream movement.

*Out-migration mark-recapture study.*—To examine Burbot out-migration from Bull Lake and identify whether out-migration was related to flow regime, we conducted a mark-recapture survey during 2 years (2013 and 2014). We sampled out-migrating Burbot with large and small trap nets (H. Christiansen Net Co., Duluth, Minnesota) that had rectangular box openings, wings off the sides of the openings, and a series of funneled hoops leading to the cod end. The large nets had 1.91-cm mesh, 1.22- × 1.83-m openings, and 1.22- × 7.62-m wings; the small nets had 0.32-cm mesh, 0.69- × 0.99-m openings, and 0.69- × 3.81-m wings. We anchored nets with t-posts with the wings angled upstream at an angle that produced total opening widths of 12.50 and 7.01 m for the large and small nets, respectively.

We selected three trap-netting sites on Bull Lake Creek: 140, 500, and 830 m below Bull Lake Dam. Up to 44% of the channel width was blocked (up to three large nets and three small nets). We set nets (three nights on, three nights off) from May 16 to August 21, 2013. We conducted two additional three-night net sets, one starting September 14 and one starting November 8, 2013. During 2014, trap-netting in Bull Lake Creek was conducted continuously from May 14 to August 19 (Table 1).

*Burbot processing and tagging.*—Captured Burbot were weighed, measured, and checked for a PIT tag by using a DataTracer FDX/HDX reader (Oregon RFID, Portland, Oregon). All untagged Burbot over 50 mm TL were given an 8-mm, full-duplex PIT tag (Oregon RFID). To mark Burbot under 50 mm, we removed the left pelvic fin. We anesthetized Burbot with Aqui-S 20E (Aquatactics, Kirkland, Washington) before fin clipping or PIT tagging. We injected PIT tags into the body cavity ventrally just ahead of the vent by using an Oregon RFID injector needle and syringe. We packed injection wounds with a 50/50 mixture of antibiotic ointment and denture fixative to prevent infection. Burbot were then allowed to return to a fully

active state in live-pens before release directly downstream from their individual capture sites.

We placed a water temperature logger (Onset Hobo U20-001-01; Onset Computer Corp., Bourne, Massachusetts) in Bull Lake Creek. Flow data were obtained from U.S. Geological Survey gauging station 06225000. In 2014, we used a Hach flow meter (Model FH950.0; Hach Company, Loveland, Colorado) and a top-set wading rod to take water depth and velocity measurements at the opening of each trap net at the beginning and end of each sampling day.

We calculated CPUE as fish per net-hour for each day of sampling. Because catch rates could be highly influenced by flow, we also calculated a volume-standardized catch rate in 2014 by estimating the number of Burbot (all ages) caught per cubic meter of water sampled per day as well as the number of age-0 Burbot caught per cubic meter per day. We created length frequency histograms and compared size distributions between years by using a *t*-test. We used linear regression to identify statistical relationships between flow or temperature and CPUE (both years) or volume-standardized Burbot and age-0 Burbot catch rates (2014 only). We included year as a random effect in the CPUE versus flow and temperature models. All analyses were conducted in R (R Core Team 2014).

*Otolith strontium study.*—We used otolith strontium isotope ratios ( $^{87}\text{Sr}/^{86}\text{Sr}$ ) to identify natal origins of individual Burbot collected from within the irrigation network. Otolith strontium isotope ratios are widely used to track the movements of individual fish because strontium isotopes are incorporated into otoliths in direct proportion to ambient water, and strontium substitutes for calcium in otolith formation (Thorrold et al. 1998; Bath et al. 2000; Kennedy et al. 2002).

Water strontium isotope ratios reflect the strontium isotope ratios of the bedrock underlying the water body and are highly stable over seasons and years (Kennedy et al. 2000, 2002). We collected one water sample from all potential source population waters (Bull, Torrey, Ring, Trail, Upper Dinwoody, and Lower Dinwoody lakes) and the Wyoming Canal, Pilot Butte Reservoir, upper Wind River (~1 km upstream from the Dinwoody Creek confluence), and lower Wind River (immediately above the Wind River

TABLE 1. Bull Lake Creek trap-netting results. Net-hours are the total hours for which all nets were in place during the sampling season. Age-0 Burbot were individuals under 100 mm. The CPUE is the number of Burbot per net-hour for each day. Standardized catch rate is the number of Burbot caught per volume of water sampled each day (calculated for 2014 only).

Year	Net-hours		Burbot captured			CPUE		Standardized catch rate	
	Small net	Large net	Small net	Large net	Age 0 (%)	Mean	Maximum	All	Age 0
2013	20,464	20,464	14	15	3	0.004	0.031		
2014	11,371	9,313	44	10	87	0.008	0.156	$5.66 \times 10^{-9}$	$1.27 \times 10^{-7}$

Diversion Dam) on October 17, 2015. Within 48 h of collection, samples were filtered through a 0.45- $\mu\text{m}$ , sterile syringe filter and were refrigerated until analysis for  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios at the Inductively Coupled Plasma Mass Spectrometry Laboratory, Department of Geology and Geophysics, University of Utah, following methods outlined by Brennan et al. (2015). We used a multi-collector (MC) inductively coupled plasma (ICP) mass spectrometer (MS; high-resolution NEPTUNE, Thermo Scientific, Bremen, Germany) and the University of Utah's introduction system to purify strontium for  $^{87}\text{Sr}/^{86}\text{Sr}$  ratio analysis of aqueous solutions. Using these methods, Brennan et al. (2015) found the long-term replicability of the NIST (National Institute of Standards and Technology) SRM987 standard ( $^{87}\text{Sr}/^{86}\text{Sr} \pm 95\%$  confidence interval =  $0.71034 \pm 0.00026$ ; [www.nist.gov](http://www.nist.gov)) to be  $^{87}\text{Sr}/^{86}\text{Sr}$  ( $\pm 2$  SDs) =  $0.71030 \pm 0.00004$ . During the water sample analysis reported here, the weighted daily average of the NIST SRM987 ratio was  $0.71029 \pm 0.000033$  ( $\pm 2$  SDs;  $n = 5$ ).

For assignment analysis, we used a nominal assignment approach in which we defined a set of candidate geographic locations of origin, and fish were assigned to the location most consistent with their otolith natal region's  $^{87}\text{Sr}/^{86}\text{Sr}$  ratio (Wunder 2012). We chose this approach over more recent model-based approaches that create a strontium isoscape with values for all possible geographic locations (Brennan et al. 2016) because our study was focused on distinguishing between a set number of locations (individual tributary lakes and the Wind River). We created strontium isotope groups on the basis of similarity in  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios and geographic patterns (Brennan et al. 2015). Upper Dinwoody Lake ( $^{87}\text{Sr}/^{86}\text{Sr} = 0.72344$ ) and Bull Lake (0.71729) were their own groups; Lower Dinwoody (0.72992), Torrey (0.73066), Ring (0.73006), and Trail (0.72997) lakes were averaged into a Torrey/Lower Dinwoody group; and the upper Wind River (0.71061), lower Wind River (0.71179), Pilot Butte Reservoir (0.71242), and Wyoming Canal (0.71181) were averaged into a Wind River group. Strontium isotopic signatures among the Torrey, Ring, Trail, and Lower Dinwoody lakes were likely indistinguishable due to similar underlying granitic bedrock. Upper Dinwoody Lake may have had a different strontium signature than Lower Dinwoody Lake due its smaller volume (i.e., short residence time) and higher levels of foreign sediment deposition from a headwater glacier. All strontium isotope groups differed from one another by at least 0.0048, and all sites within each group did not differ by more than 0.0018.

We acquired Burbot otoliths from potential source populations in Bull ( $n = 5$ ), Torrey ( $n = 3$ ), Upper Dinwoody ( $n = 5$ ), and Lower Dinwoody ( $n = 4$ ) lakes and from unknown-origin fish in the Wind River ( $n = 2$ ) and the irrigation network waters (Pilot Butte Reservoir,  $n = 12$ ; Pilot Butte Canal,  $n = 37$ ; Wyoming Canal,  $n = 18$ ). The

Wyoming Game and Fish Department and the U.S. Fish and Wildlife Service collected all Burbot from the Torrey Creek, Dinwoody Creek, and Bull Lake Creek drainages, as well as from Pilot Butte Reservoir, during other sampling projects between April 2013 and October 2014. We collected Burbot from the Wyoming and Pilot Butte canals using backpack or bank electrofishing immediately after the canal systems were shut down at the end of irrigation seasons (late September). We were unable to find any Burbot in the Wyoming Canal during fall 2013 despite extensive effort ( $>9$  h of electrofishing), but we collected 18 Burbot during fall 2014 with minimal effort ( $<3$  h of electrofishing). We sampled for Burbot throughout the 48 km of the Wind River that contained likely Burbot habitat (i.e., between the Dinwoody Creek confluence and the Wind River Diversion Dam) by using raft electrofishing during the fall in 2013 and 2014 when water was low and clear, offering the best sampling conditions. Due to the scarcity of Burbot in the river, we sampled several reaches within the total 48 km multiple times. We collected otoliths from both juvenile and adult unknown-source Burbot, but all source-population Burbot were adults.

Burbot were kept frozen until otoliths were extracted in the laboratory. We removed both sagittal otoliths, but we used the left otolith for analyses unless it was damaged or lost. Otoliths were handled only with gloves and plastic forceps. After extraction, we cleaned the otoliths, sonicated each one in MilliQ water for 3 min, and embedded them in Epofix two-part embedding resin (Electron Microscopy Supplies, Hatfield, Pennsylvania). We then transversely sectioned the embedded otoliths using a low-speed saw and two diamond-metal bonded wafering blades separated by a 1-mm-thick plastic disk. We ground the otolith sections using 2,000-grit sandpaper to a thickness less than 0.8 mm wherein the entire core surface was exposed. Otoliths were then polished with aluminum oxide grit polishing paper, decreasing in thickness to 1  $\mu\text{m}$ . We mounted the otoliths on glass slides using a small amount of cyanoacrylate adhesive. Immediately before isotopic analysis, the slide-mounted otoliths were sonicated for 5 min in MilliQ water.

We measured strontium isotope ratios ( $^{87}\text{Sr}/^{86}\text{Sr}$ ) within the otolith core by using laser ablation with a 193-nm excimer laser and the high-resolution Neptune MC-ICP-MS at the Inductively Coupled Plasma Mass Spectrometry Laboratory, University of Utah. We ablated nonlinear paths placed to avoid any nonnatal structure. Ablation paths were set within the light-colored core surrounding the primordia, staying inside of the first darker colored daily growth increments (Wright et al. 2002). The paths were curved in order to ablate enough material within this small area, and care was taken to ensure that the path did not intersect itself. We were not concerned with avoiding pre-hatch maternal influences, as barriers prevented

parents from different populations from entering any of the source populations. Our ablation settings were modeled after those of Brennan et al. (2015). We used a 53.1- $\mu\text{m}$ -diameter circle, a pulse rate of 10 Hz, a scan rate of 2  $\mu\text{m/s}$ , and a laser energy of 45%. We set transects within the core for a length equal to 190 cycles. We pre-measured transect background intensities ( $V$ ) of each isotope for 120 cycles by using the mean as a blank correction during the run. To determine the accuracy of the laser ablation runs, we ablated six to twelve 190-cycle transects of a modern marine shell before each set of 6–10 otolith transects. If shell  $^{87}\text{Sr}/^{86}\text{Sr}$  ratio means were not similar to the global marine value ( $0.70918 \pm 0.00006$ ), the Neptune MC-ICP-MS was re-tuned and shell samples were re-run before continuing with ablations.

We assigned all fish to a population or group of populations by using our strontium isotope groups as the candidate geographic locations of origin with discriminant analysis via the equation

$$P(l|i) = \frac{P(i|l)}{\sum_{l=1}^L P(i|l)}.$$

The probability that location  $l$  (given fish isotope value  $i$ ) is the natal origin is equal to the probability density of isotope value  $i$  given location  $l$ , divided by the sum of the probability densities for all potential locations (Wunder 2012). We assumed that the sampling distribution was a normal distribution for each geographic location, with the mean being the water  $^{87}\text{Sr}/^{86}\text{Sr}$  ratio of the site group. We set the SD at 0.0035, which is the highest calculated SD for  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios of fish from a capture location (Torrey Lake, SD = 0.0010; Bull Lake, SD = 0.0014; Dinwoody lakes, SD = 0.0035). This is likely highly conservative, as the Dinwoody lakes fish were unusual in their high level of variation. We assumed that the prior probability distribution was uniform over the set of locations. Fish were assigned to the location that had the highest posterior probability. We ran the model with alternative SD values and found that assignment was consistent.

*Genotyping-by-sequencing study.*—We used genomic analysis to assess Burbot population structure, which provided insight into historical movement patterns and connectivity of populations. We took tissue samples for genetic analysis (fin clips) from Burbot collected for the otolith study. In addition, we included Burbot collected by the Wyoming Game and Fish Department and the U.S. Fish and Wildlife Service between 2011 and 2013 during routine trammel-net sampling. Our goal was to sample at least 30 Burbot from each location, but scarcity of Burbot at some sites limited our sampling. We took genetic samples from fish in potential source populations within Torrey ( $n = 37$ ), Ring ( $n = 13$ ), Trail ( $n = 25$ ), Upper Dinwoody ( $n = 41$ ),

Lower Dinwoody ( $n = 17$ ), and Bull ( $n = 35$ ) lakes. We also collected additional genetic samples from fish of unknown origin in Pilot Butte Reservoir ( $n = 43$ ) and Pilot Butte Canal ( $n = 80$ ). Fin clips from all individuals were stored in ethanol until used for DNA extraction.

We extracted DNA and prepared genomic libraries for all individuals as described by Underwood et al. (2016; the library preparation method was originally described by Parchman et al. 2012). Individuals represented in genomic libraries included those from the Underwood et al. (2016) study, with the addition of Pilot Butte Reservoir, Pilot Butte Canal, and Wyoming Canal. Genomic libraries were sequenced at the Genome Sequencing and Analysis Facility, University of Texas, on the Illumina HiSeq 2500 platform, resulting in 100-base-pair, single-end DNA sequences (“reads”).

We obtained 182,798,394 reads that passed contaminant filtering and matched to a barcoded individual. Because no reference genome was available for Burbot, we used “smng” (SeqMan NGen; DNASTar) to conduct a de novo assembly of 25 million sequences to create an artificial reference genome of 53,789 contigs. We then used “bwa” (Li and Durbin 2009) to assemble all short-sequence reads to the reference genome. We excluded individuals with less than 2,000 assembled reads from further analysis.

We identified 17,863 single-nucleotide variants using “samtools” and “bcftools” (Li and Durbin 2009). We only used variant sites where at least 50% of all individuals had at least one read at that site. We also restricted sites to those single-nucleotide polymorphisms (SNPs) with minor allele frequencies greater than 1%. To ensure independence of loci, we randomly selected one site per contig. We retained 8,875 SNPs for genetic analyses.

We used a hierarchical Bayesian clustering analysis, “entropy” (Gompert et al. 2014), to classify each individual fish’s ancestry. We ran models with one to five genetic clusters ( $k = 1-5$ ) to estimate  $q$ , or the proportion of each individual fish’s ancestry that came from each of the  $k$  genetic clusters. To compare among models with different values of  $k$ , we used the deviance information criterion (DIC) to assess model fit. We also conducted principal components analysis (PCA) to identify population genetic structure without any a priori expectations about cluster membership of individuals. Using genotype probabilities from all individuals at each locus, we created a covariance matrix of genetic similarity among individuals and used this matrix in the PCA (“prcomp” in R; R Core Team 2014). These two methods complement each other, as they have very different underlying assumptions, but both identify similar patterns of genetic variation among the populations in this study.

*Genotyping by sequencing and otolith strontium comparison.*—For Burbot with both genomic and otolith microchemistry data (Torrey Lake,  $n = 3$ ; Upper Dinwoody Lake,  $n = 5$ ; Lower Dinwoody Lake,  $n = 4$ ; Bull

Lake,  $n = 5$ ; Pilot Butte Reservoir,  $n = 12$ ; Pilot Butte Canal,  $n = 25$ ), we plotted the probability of assignment to distinguishable strontium groups against proportion of ancestry in each of four genetic clusters to visualize the relationship between an individual's collection site, natal origin, and genetic ancestry. We also calculated and compared our time and material and analysis costs for the three approaches (genotyping by sequencing, otolith strontium, and out-migration netting).

## RESULTS

### Out-Migration Mark-Recapture Study

In 2013, we captured a total of 29 Burbot, with two recaptures (Table 1). Both recaptures were at the same site

as their original capture. In 2014, we captured 54 Burbot, with no recaptures. Burbot mean size was significantly larger ( $t = 11.96$ ,  $df = 80.28$ ,  $P < 0.001$ ) in 2013 (mean = 373.3 mm) than in 2014 (mean = 96.4 mm; Figure 2). In 2013, age-0 (<100-mm) Burbot made up 3.4% of our total catch compared to 87.0% in 2014.

The CPUE was higher in 2014 than in 2013 (Table 1; Figure 2); CPUE was positively correlated with flow ( $P = 0.04$ ), but not with temperature ( $P = 0.44$ ). For 2014 volume-standardized catch rates, there was no correlation with flow ( $P = 0.49$ ) or temperature ( $P = 0.85$ ) for all Burbot. However, for age-0 fish, there was a positive correlation with flow ( $P = 0.02$ ) but not temperature ( $P = 0.52$ ).

There was no significant difference in mean flow between years ( $P = 0.39$ ), although the pattern of the

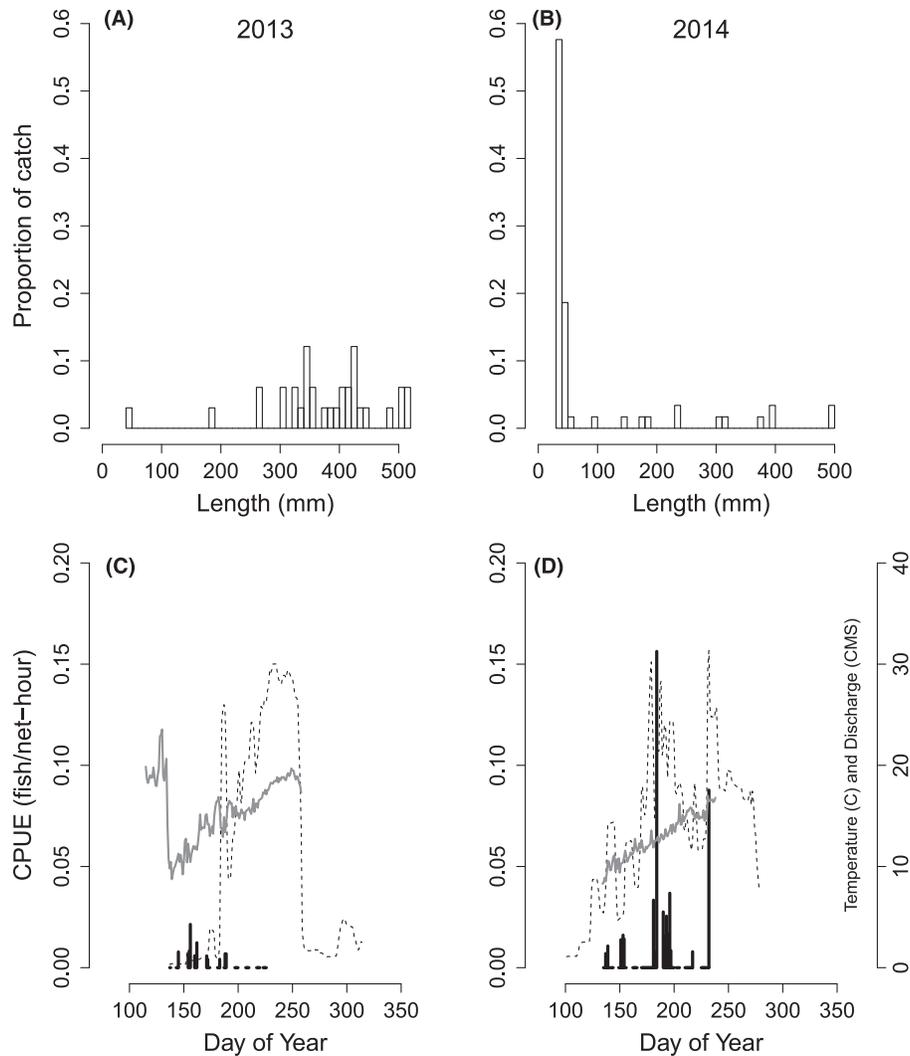


FIGURE 2. Young-of-the-year Burbot (<100 mm) made up a lower proportion of catch in Bull Lake Creek in (A) 2013 than in (B) 2014. Burbot CPUE (fish/net-hour; black bars) was lower in (C) 2013 than in (D) 2014. In Bull Lake Creek, CPUE was correlated to flow ( $m^3/s$ ; dashed black line) but not temperature ( $^{\circ}C$ ; gray line; C and D).

hydrographs varied (Figure 2). The timing of temperature increases was similar in both years, but temperatures were significantly warmer in 2013 (mean temperature in 2013 = 14.03°C; mean temperature in 2014 = 12.92°C;  $P = 0.001$ ).

### Otolith Strontium Study

We analyzed 86 otoliths for natal region  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios. Of the 17 source location otoliths, the five fish that were captured in Bull Lake were assigned to Bull Lake, while the remaining 12 fish (Dinwoody lakes and Torrey Lake fish) were assigned to the Torrey/Lower Dinwoody strontium isotope group (Figure 3). All of the unknown-population fish were either assigned to the Bull Lake strontium group or the Wind River strontium group. Fish sampled in Pilot Butte Canal and Pilot Butte Reservoir were largely assigned to the Wind River strontium group, which includes the irrigation waters, although two fish from Pilot Butte Canal were assigned to the Bull Lake strontium group. Wyoming Canal fish were mostly assigned to the Bull Lake strontium group ( $n = 14$ ), but four were assigned to the Wind River strontium group. Of the two Wind River fish, one was assigned to the Bull Lake strontium group, and the other was assigned to the Wind River strontium group.

### Genotyping-by-Sequencing Study

We identified 8,875 SNPs from 266 individuals, which were used for all genetic analyses. For the retained SNPs, mean sequence coverage was 12.6 reads per locus per individual.

In the PCA, principal component 1 separated Torrey Lake Burbot from all other populations and explained

53.5% of the genetic variation among individuals (Figure 4). Principal component 2 distinguished among Dinwoody, Bull Lake, and Pilot Butte fish and explained 16.1% of the genetic variation among individuals. For the “entropy” genetic clustering model, the model for  $k = 1$  (one genetic cluster) had the strongest statistical support ( $\text{DIC} = 7.0 \times 10^6$ ), but models for  $k = 2$  to  $k = 4$  were similarly well supported (2 clusters,  $\text{DIC} = 8.8 \times 10^6$ ; 3 clusters,  $\text{DIC} = 10.4 \times 10^6$ ; 4 clusters,  $\text{DIC} = 11.4 \times 10^6$ ) and identified additional genetic divisions in the data that are useful for identifying genetic origins of individual fish (Figure 5). These fine-scale genetic subdivisions among Wind River Burbot populations were also supported by the PCA results (Figure 4), reinforcing our confidence that our estimates of ancestry at  $k = 4$  represent real genetic differentiation among populations. Estimates of  $q$  from the  $k = 4$  “entropy” model allowed us to distinguish genetically among potential source populations (Torrey, Dinwoody, and Bull lakes) and also to identify a genetically distinct irrigation population (Pilot Butte Reservoir and Pilot Butte Canal).

### Genotyping by Sequencing and Otolith Strontium Comparison

The majority of fish caught in the Wyoming Canal, along with two Pilot Butte Canal fish and one Wind River fish, had a high probability of Bull Lake genetic ancestry and natal origin, suggesting that they were migrants from Bull Lake (Figure 6A). Two Wyoming Canal fish and one Pilot Butte Canal fish had a high probability of Bull Lake ancestry but a low ( $<0.5$ ) probability of Bull Lake isotopic origin, suggesting that their ancestors were from Bull Lake, but the individuals we sampled were spawned

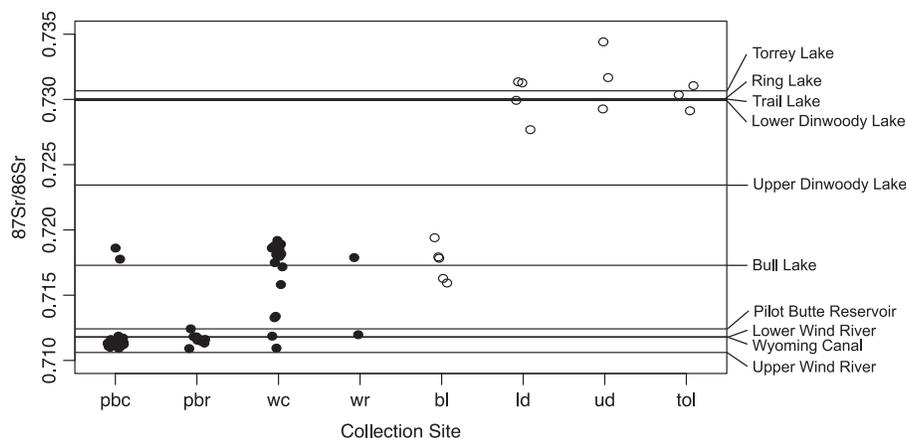


FIGURE 3. Otolith natal strontium isotope ratios ( $^{87}\text{Sr}/^{86}\text{Sr}$ ) for individual Burbot collected at locations of unknown (filled circles) and known (open circles) natal origin plotted with measured strontium ratios of water samples from potential source waters, denoted as horizontal lines. Unknown-natal-origin collections from Pilot Butte Canal (pbc), Pilot Butte Reservoir (pbr), the Wyoming Canal (wc), and the Wind River (wr) clustered with Bull Lake or the Wind River group. Potential source population collections from Bull Lake (bl), Lower Dinwoody Lake (ld), Upper Dinwoody Lake (ud), and Torrey Lake (tol) clustered with Bull Lake or the Torrey/Lower Dinwoody group.

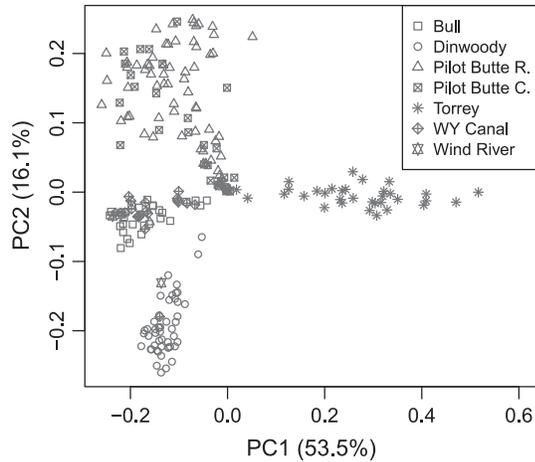


FIGURE 4. Genetic differentiation exists among Wind River Burbot populations, as shown by the first two principal components of genetic variation (PC1 and PC2; parenthetical percentages indicate amount of genetic variation explained by each axis) based on principal components analysis for the genetic covariance of individuals. Clusters of individuals from the natural populations (Bull Lake, Upper and Lower Dinwoody lakes, and the Torrey Creek lakes) are independent of each other, while individuals from Pilot Butte Reservoir (R.) and Pilot Butte Canal (C.) mostly make up a fourth cluster, suggesting isolation and reproduction within those waters. However, a number of individuals from Pilot Butte Reservoir and Pilot Butte Canal as well as the Wyoming (WY) Canal cluster with individuals from Bull Lake, indicating that some of the fish in the irrigation network originated from Bull Lake.

within the Wind River or the irrigation system. For Pilot Butte Reservoir and Pilot Butte Canal fish, the probability of isotopic origin was consistent with the Wind River, but the probability of ancestry was more variable, though distinct from other potential source populations (Figure 6B). Torrey and Dinwoody fish varied in their probabilities of genetic ancestry but were similar for isotopic origin (Figure 6C, D).

### Multiple Method Feasibility

The out-migration study was the most time consuming and expensive, as it required two employees to be in the field for 3–4 months in two different years and the nets were expensive (Table 2). Otolith and genetic analyses both took far less time, although otolith preparation and analysis took three times as long as the genetic analyses. Genetic analyses were also the cheapest but required the most specialized equipment and computational power and knowledge.

## DISCUSSION

Entrainment, or entrapment of fish within human-made water bodies, is a serious issue for fisheries management and conservation as rivers and streams are modified to facilitate human water use (Schrank and Rahel 2004;

Unwin et al. 2005; Gale et al. 2008). When fish are discovered trapped in an inappropriate habitat like an irrigation canal, it is important to identify the source of these individuals to prevent future entrainment and to assess the effects on source populations due to the loss of these fish (Post et al. 2006; Carlson and Rahel 2007; Walters et al. 2012). However, as our current study demonstrates, the origin of entrained individuals may be unexpected, and multiple methods may be required to accurately assess movement of fish.

We found evidence of entrainment of Burbot from Bull Lake into the irrigation system, but the numbers of entrained individuals from that source were very low in the years studied. Instead, we found that most Pilot Butte Canal fish were genetically distinct from potential natural source populations. These individuals likely come from a self-sustaining population within Pilot Butte Reservoir, contradicting prior speculation that the irrigation populations were primarily sustained through entrainment. We do not know how common it is for self-sustaining populations to occur within an irrigation network. Fish establishment within an irrigation network has been previously documented (Woodford et al. 2013), but most previous studies on entrainment have concluded that irrigation networks are sink habitats where survival is very low and where reproduction is not possible (Roberts and Rahel 2008).

We did not find strong support for our hypothesized mechanism that high flow releases from Bull Lake Dam were leading to Burbot out-migration. In 2013, there was almost no age-0 Burbot out-migration, and most of the individuals caught were likely adult residents of Bull Lake Creek. In 2014, there was a greater age-0 out-migration that was positively correlated to flow, suggesting that in some years, high flow releases could lead to increased Burbot out-migration. Based on historical U.S. Geological Survey gauging station data, 2014 was a relatively average discharge year, but 2013 was lower than average. Historically, there have been years with short discharge peaks nearly double what we saw during our study, and it is possible that out-migration could be higher during such events. Loss of recruitment via dam discharge has been found to decrease reservoir fish populations in other studies and has been correlated to the discharge regime (Walburg 1971; Smith and Andersen 1984; Travnicek et al. 1993). However, these losses are often equally or more strongly dependent on reservoir level, with several studies finding higher out-migration rates when reservoirs are low (Smith and Andersen 1984; Keefer et al. 2011). Bull Lake was relatively full during both study years. Although we did not look at reservoir level in relation to out-migration, it is possible that more Burbot may be flushed from the lake during years with larger drawdowns.

The higher age-0 out-migration from Bull Lake in 2014 corresponded to higher entrainment in the Wyoming

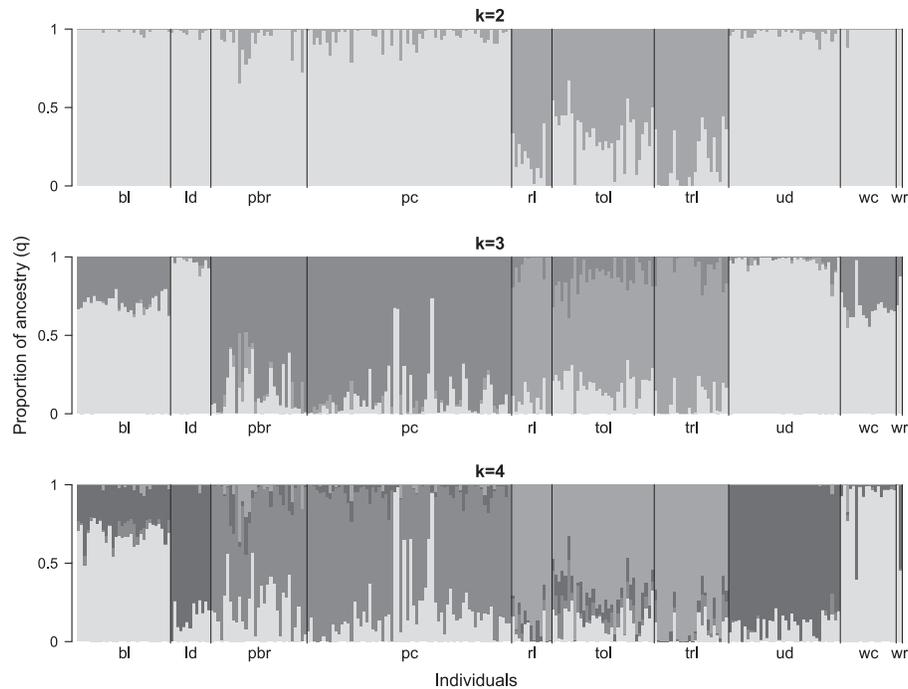


FIGURE 5. Genetic differentiation among Wind River Burbot populations is supported by the proportion of ancestry ( $q$ ) estimated by a Bayesian hierarchical model, “entropy,” under models with  $k = 2, 3$ , or  $4$  genetic clusters. Proportion of ancestry ( $q$ ) was estimated for each individual fish ( $x$ -axis; each individual’s ancestry is given by a single vertical bar) sampled from Bull Lake (bl), Lower Dinwoody Lake (ld), Pilot Butte Reservoir (pbr), Pilot Butte Canal (pc), Ring Lake (rl), Torrey Lake (tol), Trail Lake (trl), Upper Dinwoody Lake (ud), the Wyoming Canal (wc), and the Wind River (wr). Four main groups are evident: Torrey Creek (rl, tol, and trl), Dinwoody (ld and ud), Bull Lake, and Pilot Butte (pbr and pc). Some individuals captured from Pilot Butte Reservoir, Pilot Butte Canal, Wyoming Canal, and the Wind River shared ancestry with Bull Lake Burbot, and fewer shared ancestry with the Dinwoody group.

Canal during 2014 (18 sampled) compared to 2013 (0 sampled). However, the low observed levels of out-migration from Bull Lake do not align with the high levels of entrainment in Pilot Butte Canal (e.g., >1,000 Burbot in October 2014; Underwood 2015) that were observed during both years of our study period, suggesting that Bull Lake was not the primary source of Burbot entrained in Pilot Butte Reservoir and Pilot Butte Canal.

This is further supported by the otolith  $^{87}\text{Sr}/^{86}\text{Sr}$  data. There was evidence of out-migration from Bull Lake, with 1 Wind River fish, 2 Pilot Butte Canal fish, and 14 Wyoming Canal fish having  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios that matched Bull Lake, suggesting that they were born in Bull Lake. However, the majority of the Burbot collected from Pilot Butte Canal (35 fish) and all of the Burbot obtained from Pilot Butte Reservoir were assigned to the Wind River strontium group, which includes the irrigation waters. It is possible that these Burbot were entrained from the Wind River, but the most probable source is reproduction within the irrigation system. Reproduction of Burbot in Pilot Butte Reservoir could sustain the high densities of entrained Burbot in Pilot Butte Canal, and we documented the presence of larval Burbot in the reservoir during summer 2014 (Underwood 2015). It is highly unlikely that these larval Burbot

came from another population because the feeder canal to the reservoir descends through a 280-m-long, steep concrete flume, and the turbulence and abrasion in the flume are likely fatal to delicate larval Burbot.

Reproduction in Pilot Butte Reservoir does not explain the presence of four Burbot in the Wyoming Canal with strontium ratios matching the Wind River group since there are no connections from Pilot Butte Reservoir to the Wyoming Canal. The most likely natal origin for these four Wyoming Canal Burbot is the main-stem Wind River. We did catch one Burbot in the Wind River with an  $^{87}\text{Sr}/^{86}\text{Sr}$  ratio matching the Wind River strontium group (Figure 3), suggesting that some Wind River recruitment may be occurring; however, our extensive sampling of the Wind River indicates that Burbot within the river are rare. We believe that this is true and not an artifact of sampling method, as we sampled the Wind River using habitat-targeted electrofishing, which was one of the most effective methods identified for capturing Burbot in a very similar river in the region (Klein et al. 2015).

We found support for genetic differentiation among upper Wind River basin Burbot populations. The most surprising result was that Pilot Butte Reservoir and Pilot Butte Canal were genetically distinct from natural

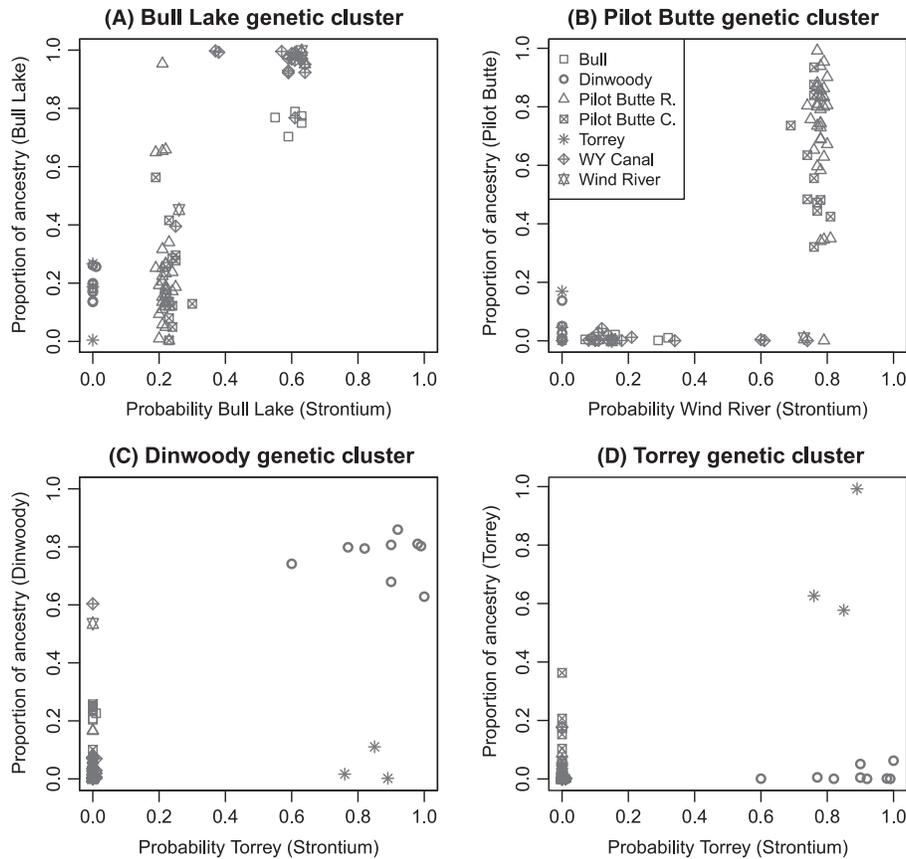


FIGURE 6. Origins of individual Burbot that were collected in waters (symbols) other than their ancestral populations are identified through the individual probability of assignment to distinguishable strontium groups (i.e., natal origin; Bull Lake, Wind River, and Torrey) plotted against each individual fish's proportion of ancestry in four distinct genetic clusters (Bull Lake, Pilot Butte, Dinwoody, and Torrey): (A) probability of assignment to Bull Lake natal origin versus proportion of ancestry in the Bull Lake cluster; (B) probability of assignment to Wind River natal origin versus proportion of ancestry in the Pilot Butte cluster; (C) probability of assignment to Torrey natal origin versus proportion of ancestry in the Dinwoody cluster; and (D) probability of assignment to Torrey natal origin versus proportion of ancestry in the Torrey cluster. Some movement between the Bull Lake (A) and Wind River waters (B) occurs, while little to no movement into or out of the Dinwoody (C) and Torrey (D) lakes is evident.

TABLE 2. A comparison of the inputs required for the three methods used in our study. Time is based on total hours worked by researchers and employees and does not include wait times for computer processing, thermocycling, etc. The salary total is based on researcher/employee salaries (technician: US\$11 per hour; master's student: \$8 per hour; doctoral student/consultant: \$18 per hour). The total material/analysis costs include all consumable and project-specific materials. The per-sample analysis costs refer only to the per-sample fee charged by the laser ablation and sequencing facilities. The special materials/requirements refer to nonconsumable items that were not included in the cost estimate.

Method	Time input (h)	Salary total (\$)	Total material/analysis costs (\$)	Per-sample analysis cost	Special materials/requirements
Out-migration netting	>1,500	13,300	13,000	–	Field housing, large vehicle
Otolith strontium	<300	2,100	9,800	\$100	Travel and lodging for ablation/mass spectrometry
Genotyping by sequencing	<100	1,200	2,300	~\$5 (varies with number of samples and desired coverage)	Access to molecular laboratory, high-performance computing resources, and bioinformatics expertise

populations on tributaries of the Wind River. Pilot Butte Reservoir has been in existence since 1926, so it was likely colonized by entrained Burbot from the Wind River or a tributary after construction. In Pilot Butte Reservoir, early entrainment likely established a founder population, which might have become genetically differentiated due to natural selection in a new habitat (Pearse et al. 2009) or genetic drift (Cross and King 1983). Subsequent reproduction within the irrigation population may then have diluted the effects of gene flow from newly entrained individuals from the Wind River or tributary populations. There is evidence of some ongoing entrainment from Bull Lake into Pilot Butte Canal, and the variability in genetic ancestry of Pilot Butte Reservoir and Pilot Butte Canal fish may reflect this.

### Multiple Approaches

Combining approaches can be a powerful tool for understanding the movement patterns and management needs of fish. Several studies have combined genetics and otolith microchemistry (Bradbury et al. 2008; Barnett-Johnson et al. 2010; Collins et al. 2013) or genetics and PIT tagging (Hecht et al. 2013; Kanno et al. 2014), but we believe that this study is one of the first to combine all three approaches. We found that using three methods that addressed different time scales allowed us to obtain a more complete view of movement dynamics than any method alone. Indeed, if we had omitted any of the three methods of studying movement, we would have been misled about the dynamics of Burbot movement and entrainment in the Wind River and adjacent tributaries and irrigation systems.

Previous studies using otolith strontium isotope ratios to identify natal origins of migratory fish have generally been able to accurately identify the origins of fish when all potential natal populations are known (Kennedy et al. 2000; Hobbs et al. 2005; Barnett-Johnson et al. 2008). In our otolith strontium study, however, we did not hypothesize that Pilot Butte Reservoir itself could be a source population, and while we were able to determine that entrained fish in Pilot Butte Canal were not primarily from Bull Lake or another tributary lake, our otolith strontium results did not identify the source or offer insight into historic trends. The inclusion of the genotyping-by-sequencing data suggested that the unknown source was reproduction within Pilot Butte Reservoir and that this had been occurring long enough to lead to genetic differentiation from potential source populations. The Bull Lake out-migration study—in conjunction with fish caught in Wyoming Canal that had a Bull Lake strontium signature—demonstrated that out-migration from Bull Lake could be a source of age-0 Burbot during high-flow events in some years.

In general, the strontium and genetics components of our study showed similar results, but for some fish, there

was a mismatch between strontium and genetic population assignment, as demonstrated by individuals that fell in the upper-left or lower-right quadrant of panels in Figure 6. In some cases, this was likely a result of lack of differentiation between groups for some sources. For example, fish from the Dinwoody Creek and Torrey Creek drainages could not be distinguished based on strontium but could be distinguished based on genetics. In other cases, it reflected movement of parents or recent ancestors of the sampled individuals. For example, the Wind River fish with a strontium signature matching the Wind River water was genetically most similar to the Dinwoody Creek population, suggesting that this individual was born in the Wind River but its ancestors out-migrated from the Dinwoody Creek drainage.

Combining netting, otolith microchemistry, and genetic methods may not always be appropriate for the question being asked and may not always be feasible financially or temporally (Table 2). Our field sampling was the most expensive component of our study, thus contradicting a common assumption that fieldwork is cheaper than specialized laboratory analyses, and reflects the undervaluation of our time. Alternatively, material requirements for the out-migration netting and otolith strontium study were relatively easy to meet, but we would not have been able to use the genotyping-by-sequencing approach if we had not partnered with a laboratory that had the materials, computing power, and analytical knowledge required to use this type of data. If these sorts of facilities and expertise are available, genotyping-by-sequencing methods may be the cheapest, least time-consuming methods to obtain the most complete picture of population connectivity. However, they may provide little insight if population-level genetic structuring is limited or if movements have not been occurring long enough to produce genetic changes.

### Implications and Conclusions

Our results challenge conventional assumptions about sources of entrained fish in irrigation systems, given that fish from natural populations in tributary lakes are not the current source of Burbot entrained in Pilot Butte Canal. In fact, the construction of the irrigation network and Pilot Butte Reservoir created a novel habitat that entrained individuals were able to colonize. This contrasts with the historical view of irrigation networks as a sink habitat (Roberts and Rahel 2008) and suggests a more complicated relationship between fish entrainment in irrigation waters and fisheries management. Because Pilot Butte Reservoir is an entirely artificial habitat, the entrainment of fish from the reservoir into the canal is less of a management concern than if the entrained fish were coming from a natural population in one of the tributaries. The large numbers of Burbot entrained in Pilot Butte

Canal do not represent a substantial demographic threat to the natural populations.

However, entrainment of Burbot from natural populations via the Wind River Diversion Dam is still an issue that may require further assessment. We documented the entrainment of Bull Lake fish into the Wyoming Canal in 2014, suggesting that at least in some years, entrainment into irrigation waters could be a concern. In addition, we found high densities of numerous other species (e.g., Salmonidae and Catostomidae) entrained in both the Wyoming and Pilot Butte canals. Future research might want to focus more on the Wyoming Canal and monitor yearly variation in entrainment rates and potential population-level effects of this entrainment.

Our results also provide insight into another management challenge: where to place salvaged Burbot. In the past, Burbot salvaged from Pilot Butte Canal were placed in Boysen Reservoir or Ocean Lake; however, Underwood et al. (2016) found that Burbot from those waters were genetically distinct from Burbot in the irrigation system and waters above the Wind River Diversion Dam. In the future, Burbot salvaged from Pilot Butte Canal could be returned to Pilot Butte Reservoir, as Burbot are classified as at-risk in the region, so conserving all populations is a priority. Reservoir managers could also potentially reduce entrainment to the canal and eliminate the need for salvages by altering the outlet of the reservoir.

Our results also provide insight into methodological challenges of quantifying fish movement. We were better able to explain the effects of dams and water diversion on Burbot movement by incorporating multiple methods that addressed entrainment sources and mechanisms, fish movement, and alterations to natural population connectivity. Other studies may also benefit from a multiple-method approach when questions relate to both historic and current movement. Combining strontium and genetic approaches appears to be particularly promising, as the methods may be able to distinguish different groups, and mismatches between genetic identity and strontium source can help to identify recent migration. The more thorough and mechanistic understanding of fish movement patterns and the effects of dams and diversions achieved through our approach will enable resource managers to make more effective conservation plans to mitigate the effects of water development in the Wind River.

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