CHEMICALLY FINGERPRINTING
NONNATIVE FISHES IN RESERVOIRS

By
Brett M. Johnson
Department of Fish, Wildlife and Conservation Biology
1474 Campus Delivery, Colorado State University, Fort Collins, CO 80523

Brian Wolff
Department of Fish, Wildlife and Conservation Biology
1474 Campus Delivery, Colorado State University, Fort Collins, CO 80523

and

Patrick J. Martinez
U.S. Fish and Wildlife Service
764 Horizon Drive, Building B, Grand Junction, CO 81506

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KEYWORDS

Emigration, nonnative fish, northern pike, walleye, burbot, largemouth bass, black crappie, smallmouth bass, crayfish, fish control, reservoirs, Colorado River, otolith, microchemistry, strontium.

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EXECUTIVE SUMMARY

This project addressed movement of nonnative fish into river reaches of critical habitat in the Upper Colorado River basin from reservoirs known to support cool- and warmwater species of nonnative fish. These species include black crappie, burbot, largemouth bass, northern pike, smallmouth bass and walleye. Before this study, it was uncertain to what extent the presence of nonnative species in critical habitat is the result of escapement or illicit transfers from reservoirs. The project had two primary objectives: 1) evaluate the utility of otolith microchemistry for fingerprinting nonnative fish in reservoirs and determining origins of nonnative fish that appeared to have emigrated from reservoirs into critical habitat, 2) evaluate factors that contribute to risk of nonnative fish emigration from reservoirs.

Otoliths were collected from nonnative species from 15 reservoirs and 7 rivers since 2006. Otoliths that were not used for microchemical analysis were archived in air-tight microcentrifuge tubes for possible future work. Strontium isotope ratio (\(^{87}\text{Sr} / {^{86}\text{Sr}}\), “Sr ratio”) proved to be an excellent natural tracer for studying fish provenance. The ratio was very consistent among species in a given reservoir and temporally stable, and all reservoir signatures within a watershed (i.e., the Sr ratio of fish from a given reservoir) were unique and thus can be used to determine provenance of fish in critical habitat. In cases where fish samples are not available, we found that crayfish carapaces can provide good short term surrogates for fish otoliths, representing site-specific strontium ratios.

We found compelling evidence that nonnative fish are emigrating from several study reservoirs and may have established reproducing populations of bass, walleye and northern pike in critical habitat. We determined that behavior and life history characteristics that place fish in the proximity of either surface or subsurface releases can result in successful downstream emigration. Survival and likelihood of downstream emigration of most species was probably higher in reservoirs that spilled frequently. The majority of dams in our study were configured and operated in a manner that allows for downstream emigration of nonnative sport fish. Screens or other fish exclusion devices were not used on most of the study reservoirs’ dams, particularly on spillways. Most of the reservoirs spilled; over half of them spilled in at least 50% of years. About 60% of reservoirs spilled every other year or more and nonnative fish emigration was detected directly by sampling or indirectly from otolith signatures in most of them.

Recovery Program partners and dam managers should collaborate to find water management schemes that achieve operational objectives for each reservoir, while minimizing the likelihood of spills that could exacerbate emigration of nonnative fish from reservoirs into critical habitat. The longer that dams lack structures limiting downstream emigration, and spill frequently, the more fish emigration to critical habitat contributes to propagule pressure and increases the likelihood that more species will become established in critical habitat below dams. Until more is known about factors driving nonnative fish movement past dams, outlet barriers and altered dam operations that 1) minimize spills and 2) keep the reservoir surface as far above penstocks as practical may be effective approaches to minimizing downstream emigration of nonnative sport fish.
Introduction

An understanding of fish origins and movements, or provenance, is important to many applied issues in fisheries. Accurately distinguishing fish of wild vs. hatchery origin, discriminating evolutionarily significant units in mixed stock fisheries, tracking movements of migratory fishes and determining sources of illegally introduced or invasive fishes require tools that can differentiate individuals or groups of fishes. In the UCRB natural dispersal and unauthorized translocation of nonnative sport fish by anglers is increasing the range of these species with undesirable effects on native species (Martinez et al. 1994; Tyus and Saunders 2000; Johnson et al. 2009). Control of nonnatives is a major objective of the native fish recovery program in the UCRB, with about US$1.5M spent annually on removal and containment (Johnson et al. 2009). Control would be improved if biologists better understood the sources of nonnative fish found in critical habitat, but conventional marking and tagging methods are considered impractical given the tremendous geographic scale of the problem.

The chemical composition of otoliths has proven useful in addressing fish provenance at large spatial scales (Barnett-Johnson et al. 2008; Walther et al. 2008). Trace element analysis has been used frequently in studies of fish origins, movements and connectivity among aquatic habitats (Campana and Thorrold 2001; Munro et al. 2005; Clark et al. 2010). However, only a few elements (e.g., Sr and Ba) appear to be reliably correlated with ambient water (Bath et al. 2000; Wells et al. 2003; Gibson-Reinem 2009) and seasonal and annual variability can be high (Gillanders 2002; Bacon et al. 2004; Walther and Thorrold 2009). The use of strontium isotope ratio ($^{87}\text{Sr}/^{86}\text{Sr}$) is emerging as one of the more useful otolith constituents for tracing fish provenance in freshwater fishes (Bacon et al. 2004; Kennedy et al. 2005; Walther et al. 2008).

Strontium isotopes vary among water bodies because $^{87}\text{Sr}/^{86}\text{Sr}$ is driven by the underlying geology across landscapes and weathering effects (Kennedy et al. 2000). Strontium isotopes in otoliths are strongly correlated with the $^{87}\text{Sr}/^{86}\text{Sr}$ in ambient water (Kennedy et al. 2000; Walther and Thorrold 2006; Barnett-Johnson et al. 2008), suggesting negligible fractionation by biotic processes. The temporal stability of $^{87}\text{Sr}/^{86}\text{Sr}$ is typically greater than that of the trace elements mentioned above, mainly because $^{87}\text{Sr}/^{86}\text{Sr}$ is not influenced by environmental factors that modify concentrations of trace elements (e.g., river discharge) or their incorporation into otoliths (e.g., temperature and salinity; Fowler et al. 1995). However, seasonal flow fluctuations may alter $^{87}\text{Sr}/^{86}\text{Sr}$ if these affect the relative contributions of water derived from geologically distinct portions of the watershed (Walther et al. 2011).

We examined the utility of $^{87}\text{Sr}/^{86}\text{Sr}$ in otoliths to determine origins of piscivores throughout the UCRB. Our primary goals were to evaluate: 1) distinctiveness of otolith $^{87}\text{Sr}/^{86}\text{Sr}$ from different reservoirs and subbasins (containing one or more reservoirs); 2) inter-annual variability of otolith $^{87}\text{Sr}/^{86}\text{Sr}$ within reservoirs; and 3) inter-species differences of otolith $^{87}\text{Sr}/^{86}\text{Sr}$ within reservoirs due to differential habitat use. We also tested the utility of $^{87}\text{Sr}/^{86}\text{Sr}$ for tracing origins of suspected reservoir escapees sampled in rivers below study reservoirs. Establishing the likely origin of river-caught fish in river-
reservoir systems through the $^{87}\text{Sr}/^{86}\text{Sr}$ signature of an otolith could be a highly valuable aid for managers dealing with invasive species in these systems.

Several questions arose later in the project that required additional research to improve our understanding and interpretations of strontium ratios of fish captured in rivers. The first question was: “do strontium ratios of fish sampled in the river downstream of a reservoir differ from the suspected upstream reservoir source?” We found that smallmouth bass sampled in the Green River below Flaming Gorge Dam had strontium ratios very close to those of smallmouth bass sampled from the reservoir itself. Concluding that these bass had escaped from Flaming Gorge Reservoir, and thus that the reservoir was a source of smallmouth bass in that part of the Green River required evidence that strontium ratio of the two habitats differed. Unfortunately, making this conclusion was impossible on the basis of fish strontium ratios alone. We needed alternative measures of river strontium ratio. We investigated several alternatives, including crayfish and snails. We assumed these invertebrates were relatively sedentary and would thus possess a strontium ratio reflective of their collection site so we evaluated their potential as site-specific sentinels of river strontium ratio. We also examined age-0 smallmouth bass and water strontium signatures to address this question.

A second question, “what are the potential sources of walleye occurring in the Duchesne and Green rivers?” was stimulated by the relatively large number of walleye sampled in the Duchesne River and Utah portion of the Green River during 2006-2011. Biologists wondered if Lake Powell might be a source. We analyzed additional walleye otoliths and compared their strontium ratios to the expected ratios of Lake Powell, Starvation Reservoir, and Red Fleet Reservoir to address this question.

The third question we added in 2011 was “what are the likely sources of an apparent increase in northern pike in the Colorado and Gunnison rivers?” During routine monitoring by Recovery Program biologists in fall of 2011 nine northern pike were captured from the Colorado River (Burdick et al. 2011). Another northern pike was collected from the Redlands Fish Passage on the Gunnison River on July 5, 2011. Because a total of only 6 northern pike had been captured in the Colorado and lower Gunnison rivers during 2004-2010 (R. Burdick, unpublished data), we examined the origins of this unusual influx by means of otolith microchemical analysis.

**Study area**

Our study area encompassed most of the UCRB (Figure 1), focusing on western Colorado, northeastern Utah and southwestern Wyoming. We sampled virtually all of the reservoirs ≥ 50 ha in Colorado and Wyoming that are connected to critical habitat and contained problematic nonnative sport fish (Table 1). At the initiation of the study it was believed that Lake Powell, more than 400 km downstream of other reservoirs in the study, was not a source of nonnative fish to the Green River. Subsequently, samples from Lake Powell were analyzed to examine this possibility.

Most of the study reservoirs have been subject to illegal introductions of warmwater fish making knowledge about their microchemical signatures useful for managers seeking to better understand and curtail this activity. Sampling sites included 15 reservoirs in 7 tributary sub-basins of the UCRB, including the Colorado River (Harvey Gap and Rifle Gap reservoirs), Dolores River (McPhee Reservoir), Green River
(Flaming Gorge and Red Fleet reservoirs), Gunnison River (Crawford, Juniata, and Paonia reservoirs), Strawberry/Duchesne River (Starvation Reservoir), White River (Kenney Reservoir and Rio Blanco Lake) and Yampa River (Elkhead and Stagecoach reservoirs, and Lake Catamount) basins (Figure 1).

Most of these reservoirs are located on the periphery of the Colorado Plateau, a relatively stable physiographic province west of the Rocky Mountains. The majority of exposed rock of the basin consists of beds of Mesozoic sandstone as well as younger Cenozoic sedimentary, shale and volcanic rock. Lake Catamount, Elkhead, Flaming Gorge and Stagecoach reservoirs are within the Wyoming Basin province, Crawford and Paonia reservoirs lie within the Southern Rocky Mountains province. In general, rivers in this region are snowmelt driven, with mountain snowpack (2,100 m – 4,000 m above sea level) dictating annual hydrologic variability (Poff and Ward 1989). Most reservoirs here are located below 2,100 m and were built to capture spring runoff for agricultural and domestic use during typically dry summers. Hydraulic residence time (HRT) averaged about 1 year in our study, but ranged 0.03 – 7.20 years, generally increasing with reservoir size (Table 1).

Methods
Field collections

Initially, we chose not to analyze water samples for $^{87}\text{Sr}/^{86}\text{Sr}$, but instead to examine otoliths of fish collected from across the basin. At the time little was known about $^{87}\text{Sr}/^{86}\text{Sr}$ in reservoirs and we believed the basin’s complex geology and water management could create spatial and temporal variation in $^{87}\text{Sr}/^{86}\text{Sr}$ of water that would be expensive to evaluate. We hypothesized that rivers and reservoirs could exhibit seasonal variation in $^{87}\text{Sr}/^{86}\text{Sr}$ associated with the hydrograph and stratification. Further, interannual variation in inflow/outflow could affect each reservoir’s $^{87}\text{Sr}/^{86}\text{Sr}$ because of variation in inflow sources and water residence time. We designed a water sampling plan to test these hypotheses and found that such a study would cost an order of magnitude more than the project’s budget. Instead, we chose to examine otoliths of fish from each reservoir assuming that 1) otoliths would integrate temporal variation in water $^{87}\text{Sr}/^{86}\text{Sr}$, and 2) if distinct differences in otoliths among reservoirs were not found then knowledge of water $^{87}\text{Sr}/^{86}\text{Sr}$ would be somewhat irrelevant to the problem of tracing fish provenance.

Nine species of nonnative fish were collected opportunistically from agency biologists in cooperation with the Upper Colorado River Endangered Fish Recovery Program (Colorado Division of Parks and Wildlife, CPW; Colorado State University Larval Fish Lab, CSU-LFL; U.S. Fish and Wildlife Service, USFWS; Utah Division of Wildlife Resources, UDWR; and Wyoming Game and Fish Department, WGF) conducting sampling for the monitoring and management of nonnative piscivores during 2004 – 2011 from reservoirs and rivers throughout the UCRB (Table 2). The goal was to sample the full complement of predominantly piscivorous nonnative fishes present in each system, including: black crappie, burbot, largemouth bass, northern pike, smallmouth bass and walleye. River fish were collected from throughout each of the seven river systems in the study area. Age-1 and older fishes were euthanized with a lethal dose of MS-222, placed on ice in the field, subsequently frozen and transferred to the Colorado State University Fisheries Ecology Laboratory in Fort Collins, Colorado.
where otoliths were extracted. Overall, we processed nearly 2,000 sets of otoliths from nonnative species collected from 15 reservoirs, 1 pond, and 7 rivers during 2006-2011 (Table 3). Otoliths that were not used for chemical analysis were archived in air-tight microcentrifuge tubes for possible future work. No samples of fish were obtained from below Paonia, Crawford, Ridgway, and Stagecoach reservoirs.

To refine our understanding of river strontium signatures, we also gathered samples of crayfish, snails, age-0 smallmouth bass otoliths and water from the Upper Green River and Flaming Gorge Reservoir in 2011 (Figure 2). Crayfish were collected with baited traps set overnight near the boat ramp at Swinging Bridge in Brown's Park, Colorado and near the dam in Flaming Gorge Reservoir during September 11-16, 2011. We gathered samples of New Zealand mudsnails and water from the Green River at Swinging Bridge, the Flaming Gorge Reservoir tailwater and Little Hole downstream. Age-0 smallmouth bass otoliths were collected from Lodore by CSU Larval Fish Laboratory (Table 4). We assumed these fish were residents of the river collection location, based on their early stage of development. Crayfish were euthanized upon collection by separating the abdomen from the cephalothorax, and were placed in individual Whirl-pak bags. Mudsnails were also sealed in Whirl-paks. Samples were stored on dry ice to insure complete mortality. Water samples were collected using ultra-clean sampling methods (Shiller 2003) at Flaming Gorge Reservoir, the tailwater, Little Hole and Swinging Bridge. Water samples were stored on ice until they could be sent to WHOI for determination of strontium isotope ratio.

**Otolith preparation**

Sagittal otoliths were removed with non-metallic forceps and sonicated in Milli-Q water for five minutes. Left otoliths were used for all $^{87}\text{Sr}/^{86}\text{Sr}$ analytical work; right otoliths were only used if the left otolith was broken or lost. Otoliths were embedded in Epo-Fix™ epoxy prior to being sectioned through the core in a transverse plane on an Isomet™ low speed saw. Sections were sanded to a thickness of approximately 200 - 250 μm to expose the inner annuli, mounted onto glass slides using double-sided tape, washed with 5% ultrapure nitric acid and sonicated in ultrapure water for five minutes. Mounted otoliths were dried for 24 hours under a Class 100 laminar flow hood, and subsequently enclosed in polystyrene petri dishes prior to ablation analysis.

**Strontium isotope analysis**

Otolith thin sections were assayed for $^{87}\text{Sr}/^{86}\text{Sr}$ using a Thermo Finnigan Neptune multicollector inductively coupled plasma mass spectrometer (MC-ICP-MS) coupled to a New Wave Research UP 193 nm excimer laser ablation system at the Woods Hole Oceanographic Institution (WHOI) Plasma Mass Spectrometry Laboratory in Woods Hole, Massachusetts. The laser ablation MC-ICP-MS was configured to run at 80% intensity, 10 Hz pulse rate, 35 μm laser beam spot size, 7 μm per second laser scan speed and 550 μm laser ablation distance within annuli. Using this method, ablated otolith material was carried from the laser cell to the MC-ICP-MS via helium gas, where it was then mixed in a spray chamber with argon gas and a wet aerosol at which time a suite of isotopes were measured: $^{83}\text{Kr}$, $^{84}\text{Sr}$, $^{85}\text{Rb}$, $^{86}\text{Sr}$, $^{87}\text{Sr}$, $^{88}\text{Sr}$. According to Woodhead et al. (2005), interference on Sr isotopes can be caused by calcium (Ca) argides, Ca dimers and doubly charged erbium (Er) and ytterbium (Yb).
However, it has been demonstrated that rubidium (Rb) and krypton (Kr) isotopes create the main interferences in other $^{87}\text{Sr}/^{86}\text{Sr}$ laser ablation ICP-MS analyses (Barnett-Johnson et al. 2005; Jackson and Hart 2006; Walther et al. 2008). We adjusted for Kr and Rb interferences following the techniques described by Jackson and Hart (2006) and Walther et al. (2008) respectively. All otolith samples and standards were normalized to a daily mean of the National Institute of Standards and Technology (NIST) Standard Reference Material 987 (SRM 987; accepted $^{87}\text{Sr}/^{86}\text{Sr}$ of 0.71024) using the formula: 

$$^{87}\text{Sr}/^{86}\text{Sr}_{\text{normalized}} = \left(\frac{0.71024}{\text{SRM 987measured}}\right) \times ^{87}\text{Sr}/^{86}\text{Sr}_{\text{sample}}.$$ 

Solutions of JRS and SRM 987 produced daily mean ($\pm$ 1 SD; sample size) $^{87}\text{Sr}/^{86}\text{Sr}$ of 0.70916 ($\pm$ 0.00001; $n = 5$) and 0.71029 ($\pm$ 0.00006; $n = 9$) respectively, and ablations of marine sclerosponge produced a daily mean $^{87}\text{Sr}/^{86}\text{Sr}$ of 0.70918 ($\pm$ 0.00003; $n = 4$).

**Reservoir signatures**

A subset of 133 otoliths collected from study reservoirs during 2006-2009 was selected for detailed analysis (Table 5). These otoliths were analyzed by the "spot method"; spots were ablated within annuli to obtain year-specific $^{87}\text{Sr}/^{86}\text{Sr}$. For reservoir fishes, each otolith was ablated within the outermost annulus (hereafter, "edge") and the innermost annulus (hereafter, "core"). All core ablations were outside the primordium to minimize potential developmental or maternal influence on the otolith's $^{87}\text{Sr}/^{86}\text{Sr}$ (Chittaro et al. 2006; Mac Donald et al. 2008).

Preliminarily, we visually examined three bivariate plots to assess the importance of sub-basin, reservoir, species and year as factors affecting variation in $^{87}\text{Sr}/^{86}\text{Sr}$. A plot of $^{87}\text{Sr}/^{86}\text{Sr}$ from each reservoir was examined to determine differences among sub-basins and reservoirs – each plot shows the distribution of mean core and edge $^{87}\text{Sr}/^{86}\text{Sr}$ for each individual per location. A second plot of mean $^{87}\text{Sr}/^{86}\text{Sr}$ of reservoirs over time – by taking the average $^{87}\text{Sr}/^{86}\text{Sr}$ from all ablations corresponding to a given year, including all species – was examined for inter-annual trends and compared among reservoirs within sub-basins. Finally, a third plot of $^{87}\text{Sr}/^{86}\text{Sr}$ among species within reservoirs was also examined – generated by averaging core and edge $^{87}\text{Sr}/^{86}\text{Sr}$ of each individual and then averaging these values for all individuals of a given species.

Following our visual assessment of the data, we assessed normality of the $^{87}\text{Sr}/^{86}\text{Sr}$ for each reservoir using box-and-whisker plots and conditional studentized residuals diagnostic plots from mixed regression models (described below). Diagnostic plots did not reveal any major departures from normality. Additionally, Shapiro-Wilk tests (PROC UNIVARIATE, SAS®) failed to reject normality of studentized residuals of $^{87}\text{Sr}/^{86}\text{Sr}$ from each reservoir, with the exception of Flaming Gorge Reservoir ($p = 0.02$); therefore no data transformations were performed.

We used mixed regression models (PROC MIXED, SAS®) to estimate the relative importance of reservoir, species and year as effects contributing to variation in $^{87}\text{Sr}/^{86}\text{Sr}$. We performed our analysis in three phases, principally because the sampling protocol resulted in an unbalanced dataset, as species and years were not sampled equally among reservoirs. We specified the full maximum likelihood estimation option in PROC MIXED to accommodate phase 3, an AICc analysis involving competing models and different fixed effects (Singer and Willet 2003). In the first phase we considered two models fitted with only one fixed effect, an intercept, and up to two random effects. The
purpose of this phase of our analysis was to determine important sources of variance (variance components) in $^{87}\text{Sr} / ^{86}\text{Sr}$. In the first model we fitted a random effect for each individual fish (hereafter, “FishID”), as fish could contribute data points from multiple ablations (one per annuli, core and edge). In the second model we again included FishID as a random effect, but this time we added a second random effect (hereafter, “Res x Spp x Year”) consisting of all unique combinations of reservoir, species and year. The two random effects models were ranked using Akaike's Information Criterion adjusted for small sample size (AICc). The best random effects structure was the model that included the Res x Spp x Year random effects (more below). The random effects structure from this model was maintained in all fixed effects models considered in subsequent analyses (phases 2 and 3).

In the second phase of our analysis, we estimated the variance explained by each fixed effect (reservoir, species and year) as the proportional change in the total variance when each fixed effect was added to the Res x Spp x Year model from phase one. The approach, deploying variance components, enabled us to determine the amount of variation attributable to (explained by) each of our fixed effects (Singer and Willet 2003).

In the third phase we evaluated, using AICc and associated statistics, a suite of models encompassing all possible combinations of our fixed effects – reservoir, species and year. Post hoc, we also assessed a dichotomous species effect (DSE) where walleye $^{87}\text{Sr} / ^{86}\text{Sr}$ were specified as different than all other species using a 0 or 1 dichotomous variable (0 = non-walleye, 1 = walleye). Additionally, we included an interaction model for reservoir and DSE because differences were not consistent among reservoirs. To determine the relative importance of each model, delta AICc ($\Delta i$) and Akaike weights ($w_i$) were calculated for each model $i$. Delta AICc can be thought of as the amount of information lost (about the true process that produced the data) relative to the top ranked model where the top (or best) model has the lowest AICc value: $\Delta i = \text{AICc}(i) - \text{AICc(top)}$. Akaike weights or model probabilities, calculated using model likelihoods (ML), sum to one across the full model set thus provide relative support for each model: $w_i = \text{ML}(i) / \sum \text{ML}$, where $\text{ML}(i) = e^{-0.5 \times \Delta i}$. To determine the relative importance of each fixed effect, cumulative Akaike weights ($W+(j)$) were calculated for all fixed effects by summing the $w_i$ from each model that contained each respective fixed effect.

**Origins of river fishes**

Initially, we ablated otoliths from 82 fish captured in rivers during 2006-2009 (Table 6). Later, more river fish were analyzed as new management concerns were identified (Table 7-9, described below). We ablated each otolith at the core and edge. In addition, if the core and edge $^{87}\text{Sr} / ^{86}\text{Sr}$ were > 150 ppm different, then spots in additional annuli between the core and edge were ablated to establish the year when the change occurred. That year was presumed to be the time when the fish moved from a reservoir to the river. We used a compound light microscope to determine fish ages from otolith annuli and from capture date, the year corresponding with within-annulus ablations.

We were able to verify the effectiveness of otolith $^{87}\text{Sr} / ^{86}\text{Sr}$ for tracing origins of reservoir fish emigrating into rivers in the Yampa River/Elkhead Reservoir system.
Here, other investigators have been Floy tagging smallmouth bass in the river and translocating some of them (hereafter, “transplants”) into Elkhead Reservoir on a tributary to the Yampa River since 2003 (Hawkins et al. 2009). Some of these fish subsequently escaped back into the Yampa River, were recaptured. Other tagged fish that had not been translocated were later recaptured in the Yampa River (hereafter, “residents”). We examined $^{87}\text{Sr}/^{86}\text{Sr}$ from fishes exhibiting each of these capture histories.

For other species and river/reservoir systems we needed to determine, in the absence of known histories from tagging, if $^{87}\text{Sr}/^{86}\text{Sr}$ of river-resident fish differed from those in upstream reservoirs before inferring reservoir escapement. We compared predictions of each reservoir’s $^{87}\text{Sr}/^{86}\text{Sr}$ from the top ranked model (phase three from above; reservoir and dichotomous species fixed effects with interaction) to the measured core and edge $^{87}\text{Sr}/^{86}\text{Sr}$ of river-captured fish. There were two prediction interval estimates in the top ranked model, one estimate for walleye, when sampled from a reservoir (i.e., not all reservoirs had a predicted walleye $^{87}\text{Sr}/^{86}\text{Sr}$), and the other estimate for all other species. These comparisons assumed that 1) reservoir emigrants possessed a core $^{87}\text{Sr}/^{86}\text{Sr}$ similar to a reservoir’s signature unless it emigrated at a very early age before accreting a detectable reservoir signature; and 2) river-caught reservoir emigrants exhibited a river signature in their otolith edge that differed from the reservoir signature in their core unless it emigrated shortly before capture. Since many of the river-caught fishes were collected in early summer (June and July) otolith growth in that year would likely be too narrow to accommodate the ablation laser’s beam diameter. Thus, when the edge was too narrow, edge signatures measured by the ablation may actually reflect the fish’s environment in the year prior to capture. This complication notwithstanding, if the core $^{87}\text{Sr}/^{86}\text{Sr}$ of a river-caught fish was within the 95% confidence limits of the predicted estimates (top ranked model, phase three) of an upstream reservoir’s signature, we concluded that the fish could have moved to the river from that reservoir. In circumstances where river-caught fishes had overlapping $^{87}\text{Sr}/^{86}\text{Sr}$ of upstream reservoir for their entire lifetime (core and edge), then we assumed that these fish could have recently moved from the reservoir. However, with the exception of tagged fish in the Yampa River, we were unable to conclusively determine if such fish were simply river-residents from an environment that shared the same $^{87}\text{Sr}/^{86}\text{Sr}$ as the reservoir upstream. This prompted additional work in 2011 to examine site-specific river signatures (below).

Additional sets of walleye (Table 7) and northern pike (Table 8) otoliths were analyzed after it became apparent that these species were expanding their ranges in critical habitat. In the larger, subsequent sample of walleye ($N = 57$) six fish did not have enough Sr present in the otoliths to obtain valid signatures of $^{87}\text{Sr}/^{86}\text{Sr}$. These six fish were excluded from all further analyses. No walleye otoliths were available from Lake Powell so we analyzed archived otoliths of smallmouth bass collected from Lake Powell in 2004 (Table 9) for an earlier project on fish provenance (Johnson et al. 2007). We assumed that the strontium measurements from these fish were similar to contemporary signatures of walleye from Lake Powell (but there is some evidence that this assumption could be false, see below). Strontium ratios of the smallmouth bass were then used to determine if fish from that system could be distinguished from fishes from other Upper Basin reservoirs. All of these otoliths were ablated via a single transect
across the entire otolith (going over the core or natal region) to enable the reconstruction of the geochemical history throughout the lifetime of each fish. After ablation, signature profiles were then superimposed on otolith photographs to properly align the profile over each fish’s lifetime. Once aligned, the portion of each profile from the core to the edge was used to determine the movement patterns of each fish. An 8-point moving average of ablation data was used to smooth the data and facilitate analysis of trends.

Age-0 smallmouth bass otoliths, crayfish carapaces and mudsnail shells collected in 2011 were analyzed by LA-ICP-MS in the Neptune mass spectrometry facility at the Woods Hole Oceanographic Institution, in Woods Hole, Massachusetts during November 2011. Crayfish carapaces, mudsnail shells, and smallmouth bass otoliths were analyzed by laser ablation (Table 4). Water samples were analyzed by the solution method, performed by WHOI personnel.

Statistical analysis of the additional samples was less complex than that used for establishing reservoir signatures. For these samples we computed the average core and edge value of $^{87}\text{Sr}/^{86}\text{Sr}$ – calculated by taking the mean values from the center of the core out for 4 analysis-cycles (equal to 60 – 77 µm in length). We then used these values in a Quadratic Discriminant Function Analysis (QDFA) to classify fish to their likely origin, based on established baseline data, or “fingerprints”, from likely reservoir sources. Post hoc, we used a QDFA using only $^{87}\text{Sr}/^{86}\text{Sr}$ data from our entire database previously established.

**Results**

**Reservoir signatures**

Reservoir $^{87}\text{Sr}/^{86}\text{Sr}$ were not visibly clustered within sub-basins, with the exception of the Colorado sub-basin (Figure 3). Consistent with this result, pre-analysis suggested that the fixed effect of sub-basin was not statistically or biologically significant, i.e., variation in $^{87}\text{Sr}/^{86}\text{Sr}$ was a function of reservoir with no effect of sub-basin. Given these observations, sub-basin effects were excluded from subsequent analyses. Reservoir $^{87}\text{Sr}/^{86}\text{Sr}$ averaged across all individuals were distinct, particularly within sub-basins (Figure 3, 4). By averaging all ablations in a given year in each reservoir, we found that annual variation in reservoir $^{87}\text{Sr}/^{86}\text{Sr}$ was small in comparison to the differences we observed between reservoirs in the same sub-basin (Figure 5).

Lake Catamount showed the most annual variability of any reservoir in our study; however, Lake Catamount’s signature still remained distinct from the other reservoirs (Elkhead and Stagecoach) in the Yampa River sub-basin. When we visually examined possible species effects within reservoirs, only one species (walleye) showed consistent differences in $^{87}\text{Sr}/^{86}\text{Sr}$ compared to the others (Figure 6). These differences were observed only in Juniata and Starvation reservoirs (Figure 6).

Of the two random effects models examined (Table 10), the top ranked model included the random Res x Spp x Year and FishID effects (AICc = -4524.20; wi= 1.00). The competing model with only the FishID random effect had no support ($\Delta = 103.50; w = 0.00$). We maintained the random effects from the top model in our subsequent analyses. Total variance in our top random effects model was reduced by 96%, 50%, and 5% with the addition of reservoir, species and year, respectively (Table 11).
From our analysis of fixed effects (Table 10), the top ranked model included the fixed effects reservoir and species. This model attained virtually all of the model weight ($\text{AIC}_c = -4922.60; w = 0.98$). The remaining models had delta AICc values $> 7$ and the sum of the weights for these models was 0.02 or 2%. Thus, given the data, our analysis of fixed effects supported only one model, the model with reservoir and species. Cumulative Akaike weights for reservoir, species and year effects were 1.00, 1.00, and 0.02 respectively (Table 10). These results indicate that the effect of reservoir, which was also in the only model supported in our analysis of fixed effects, was strongly supported by the data. Although species had an equivalent cumulative weight as reservoirs, this effect nonetheless performed poorly in models that did not include reservoir (best species model that did not include reservoir, $\Delta \geq 361.40$). The cumulative weight for year is strong evidence that $^{87}\text{Sr}/^{86}\text{Sr}$ varied independent of year.

Our visual assessment suggested that walleye was the only species that showed differences in $^{87}\text{Sr}/^{86}\text{Sr}$ compared to other species. This suggests an alternative and more parsimonious structure for the species effect that is likely more consistent with the data; namely, a dichotomous species effect (DSE), where walleye differs from all other species examined rather than all species are different. Since the observed differences with walleye appeared in only two of five reservoirs containing walleye (Juniata and Starvation reservoirs) we also added a model with a reservoir and species interaction term. When the DSE models were added to the same set of models in phase 2, the top ranked model was reservoir and DSE fixed effects with interaction ($\text{AIC}_c = -4940.70; w = 0.99$). All of the other models had a $\Delta > 10$ and a combined $w$ of 0.01 (Table 10).

Thus, only the top model was supported by the data and the species effect was largely driven by differences in walleye compared to other species in certain reservoirs. In summary, both phases 2 (variance components) and 3 (fixed effects) suggested that the effect of year was negligible compared to reservoir and species.

**Origins of river fishes**

Change in $^{87}\text{Sr}/^{86}\text{Sr}$ of smallmouth bass translocated from the Yampa River into Elkhead Reservoir ($N = 3$) was detected in each case (Figure 7). These fish also allowed us to evaluate transitional dynamics of the $^{87}\text{Sr}/^{86}\text{Sr}$ signature. A fish moved from the river and residing for just two months in the reservoir had an $^{87}\text{Sr}/^{86}\text{Sr}$ between those of the two locations, and a translocated fish residing in the reservoir for 5 months also had an intermediate signature (Figure 7). We believe the intermediate $^{87}\text{Sr}/^{86}\text{Sr}$ were due to the intrusion of the river signature into measurements when the laser ablated portions of the otolith that included periods of both river and reservoir occupancy. The $^{87}\text{Sr}/^{86}\text{Sr}$ of a fish that resided in the reservoir for 26 months overlapped the reservoir's $^{87}\text{Sr}/^{86}\text{Sr}$, implying that a fish would need to reside in a new location for $> 5$ and $\leq 26$ months to acquire a pure $^{87}\text{Sr}/^{86}\text{Sr}$ of that location, given our methods. Ablation time series of untagged smallmouth bass captured in the Yampa River (Figure 7) showed that these fish originated from somewhere within the Yampa River itself and not from Elkhead Reservoir, suspected as the original source of reservoir smallmouth bass to the river (Hawkins and Nesler 1991; Nesler 1995). Core $^{87}\text{Sr}/^{86}\text{Sr}$ of all river-caught smallmouth bass were well outside the 95% prediction interval of the mean Elkhead Reservoir signature using the top ranked model (analysis, phase three).
Two of 10 northern pike caught in the Yampa River had core $^{87}\text{Sr}/^{86}\text{Sr}$ that fell within the 95% confidence limits of Lake Catamount $^{87}\text{Sr}/^{86}\text{Sr}$ (0.71035 – 0.71049). However, the Lake Catamount $^{87}\text{Sr}/^{86}\text{Sr}$ was similar to the $^{87}\text{Sr}/^{86}\text{Sr}$ of smallmouth bass known to have been residing in the Yampa River. Thus it is possible that these fish originated from within the Yampa River. Of the remaining 8 northern pike examined, 4 had core $^{87}\text{Sr}/^{86}\text{Sr}$ that were most consistent with several ponds in that region (R.M. Fitzpatrick, Colorado Division of Wildlife, unpublished data) and 4 other fish’s $^{87}\text{Sr}/^{86}\text{Sr}$ were slightly outside the 95% confidence limits of Lake Catamount’s signature and may have come from that source. Taking into consideration the standard error associated with each ablation’s $^{87}\text{Sr}/^{86}\text{Sr}$, three of the four previously mentioned fish would have overlapped with the Lake Catamount $^{87}\text{Sr}/^{86}\text{Sr}$ prediction interval.

In the Colorado River sub-basin, all of the smallmouth bass we examined (N = 4) appeared to be of river origin. Walleye collected in the upper Colorado River in 2006-2007 (N = 7), all appeared to have emigrated from Rifle Gap Reservoir, where four of seven otolith core $^{87}\text{Sr}/^{86}\text{Sr}$ were within the 95% confidence limits of Rifle Gap Reservoir’s $^{87}\text{Sr}/^{86}\text{Sr}$. (Figure 8). The core $^{87}\text{Sr}/^{86}\text{Sr}$ of the remaining walleye were just outside the predicted Rifle Gap Reservoir $^{87}\text{Sr}/^{86}\text{Sr}$, but subsequent growth bands fell within Rifle Gap Reservoir’s predicted signature for all but one case, until the fish appeared to move from the reservoir to the Colorado River (Figure 8). Additionally, when considering the standard error of each ablation’s $^{87}\text{Sr}/^{86}\text{Sr}$, all Colorado River walleye would have been classified to Rifle Gap Reservoir as a source location. Examination of the time series $^{87}\text{Sr}/^{86}\text{Sr}$ of individual walleye showed the time of movement occurred during 1996-1998, a period with unusually high flows in the Colorado River sub-basin (Figure 8).

Signature profiles indicated that of the 10 northern pike captured from the Colorado River in 2011, three had core signatures consistent with previously established signatures of fishes from Rifle Gap Reservoir; these fish are referred to as “movers” (Table 8; Figure 9). The remaining seven fish from the Colorado River had signatures that did not change over time, suggesting that they were either river residents or they came from an off-channel location that shares the signature of the Colorado River; these fish are referred to as “residents”. The northern pike captured from the Redlands Fish Passage (CO-1-1) had a core signature that was also consistent with Rifle Gap Reservoir. However, the fish passage is located on the Gunnison River, and that fish’s signature also matched the signature of northern pike from Paonia Reservoir upstream of the passage structure. Given our ages of the Colorado River “movers”, it is estimated that CO-1-3 and CO-1-2 escaped from Rifle Gap Reservoir sometime in early 2007 and 2008, respectively (Table 8).

In the Green River sub-basin, four of five smallmouth bass captured from the Duchesne River were classified as escapees from Starvation Reservoir based on otolith core $^{87}\text{Sr}/^{86}\text{Sr}$. However, in three of these four otolith edge $^{87}\text{Sr}/^{86}\text{Sr}$ were also consistent with Starvation Reservoir implying that either these fish recently emigrated or the signatures of the Duchesne River and Starvation Reservoir may be too similar to distinguish. Another smallmouth bass had a $^{87}\text{Sr}/^{86}\text{Sr}$ profile that did not match any sources in our study. One of five smallmouth bass was classified as having originated from Flaming Gorge Reservoir (Figure 10). However, water, crayfish carapaces and smallmouth bass otoliths sampled from Flaming Gorge Reservoir did not differ from
those sampled from four locations on the Green River, below Flaming Gorge Dam (Figure 11). Thus, Flaming Gorge Reservoir cannot be singled out as the source of this fish. It is also possible that this fish originated in the Yampa River, which had $^{87}\text{Sr}/^{86}\text{Sr}$ similar to the isotope ratios of smallmouth bass collected from the Upper Green River. Therefore, we cannot rule out the possibility that these fish came from the Yampa River or the Green River, since the otolith edge $^{87}\text{Sr}/^{86}\text{Sr}$ were similar. Shells of New Zealand mudsnails from the Green River were not useful for isolating river $^{87}\text{Sr}/^{86}\text{Sr}$ because they were highly variable and did not correspond with other measures of water strontium ratio (Figure 11).

Initially, eight of 13 walleye analyzed from the Upper Green River were classified to Starvation Reservoir, using the predicted $^{87}\text{Sr}/^{86}\text{Sr}$ of walleye from the top ranked model from phase three of the analysis and the remaining individuals fell just outside that range (Figure 10). When taking into account the standard error of each ablation’s $^{87}\text{Sr}/^{86}\text{Sr}$, all but two walleye would have been classified to Starvation Reservoir as a source location. However, as stated above, Starvation Reservoir and the Duchesne River may share similar $^{87}\text{Sr}/^{86}\text{Sr}$, so it is possible that these walleye originated from the Duchesne River. High flow in the Strawberry River in 2005 coincided with the year when many of the reservoir-origin fish were estimated to have escaped (Figure 10). However, some escapement was estimated to have occurred during low flow periods without spills (2003, 2004; see Figure 42, Part 2), which suggests that 1) our ages at entry to the river were incorrect, 2) these fish escaped through an outlet that doesn’t require reservoir spills, or 3) they arose from an unauthorized transplant.

Most of the walleye from the additional sample (43 of 52) had $^{87}\text{Sr}/^{86}\text{Sr}$ values that overlapped with both Lake Powell and Starvation Reservoir ($^{87}\text{Sr}/^{86}\text{Sr}$ values are too similar to differentiate; Figure 12). However, most had core signatures that overlapped with the Starvation Reservoir signature when adjusting for the standard deviation of walleye signatures. A QDFA with $^{87}\text{Sr}/^{86}\text{Sr}$ from our complete dataset from fishes from the Green River basin suggested that of the 51 walleye captured from the Green River, 41 had core signatures consistent with previously established signatures of fishes from Lake Powell or Starvation Reservoir, two from Red Fleet Reservoir, and the remaining nine fish from the Green River had signatures suggesting that they were river residents (Table 7). In our initial sample collected prior to 2011 (N = 13), none of the walleye were classified as river origin fish. The one walleye from the Yampa River was classified as a reservoir origin fish using $^{87}\text{Sr}/^{86}\text{Sr}$.

Profiles of $^{87}\text{Sr}/^{86}\text{Sr}$ through each fish’s lifetime revealed that most movement occurred between 568 µm and 800 µm from the core of the otolith (Figure 12); this timing of movement corresponded to about 4 years of age on average. However, some fish had profiles that did not show any evidence of movement (i.e., no change between core and edge; Figure 12) and some movements occurred at different ages (Figure 13).

Northern pike captured from the Upper Green River had very low classification rates; two of seven were classified to Flaming Gorge and Starvation reservoirs, but neither of these locations had known populations of northern pike. This suggests that most of the northern pike examined emigrated from a location outside the Green River sub-basin. These fish may have originated from the Yampa River sub-basin where northern pike are much more abundant, and Floy tagging work showed that such movements do occur (J. Hawkins, personal communication). Three of seven pike also
had an ablation that matched Lake Catamount before the edge portion of the otolith. The remaining two northern pike had $^{87}\text{Sr}/^{86}\text{Sr}$ indicating a source not sampled in this study.

In the Dolores River sub-basin $^{87}\text{Sr}/^{86}\text{Sr}$ of the core and edge of river-caught smallmouth bass overlapped with the predicted $^{87}\text{Sr}/^{86}\text{Sr}$ of McPhee Reservoir. We do not have data to address whether McPhee Reservoir and the Dolores River have similar $^{87}\text{Sr}/^{86}\text{Sr}$. Core and edge $^{87}\text{Sr}/^{86}\text{Sr}$ of smallmouth bass caught in the White River matched that of Kenney Reservoir (based on black crappie otoliths), but again, we do not have data to address whether the river and reservoir have similar $^{87}\text{Sr}/^{86}\text{Sr}$. Rio Blanco Reservoir was not indicated as an escapement source of smallmouth bass captured from the White River.

**Discussion**

Given the general distinctiveness of reservoirs, temporal stability, and lack of inter-specific effects in our findings, the $^{87}\text{Sr}/^{86}\text{Sr}$ in otoliths showed great potential as a natural tracer for provenance of reservoir piscivores. Our research also provided evidence that some reservoirs are potentially important sources of invasive piscivores in the UCRB. This was particularly true for walleye, where in every river subbasin containing the species we detected clear movement patterns from a likely reservoir source. This evidence suggested that walleye reproduction in these rivers may have been limited during the study, and therefore that this species could be controlled in critical habitat by containment of reservoir sources and suppression of riverine stocks. However, the relative contribution of potential reservoir escapees to riverine stocks has yet to be determined, and the more fish that emigrate to critical habitat may increase the likelihood of riverine reproduction. In some other cases we could not conclusively distinguish river from reservoir signatures but the method was still useful for eliminating some potential sources, allowing managers to better focus their control efforts on the most likely sources.

We found that inter-annual variability in the $^{87}\text{Sr}/^{86}\text{Sr}$ of reservoir fish from most reservoirs was negligible, at least over the nearly decadal scale of our study. Models with a year term were not well supported, based on low cumulative Akaike weight and the variance components analysis. Temporal stability of reservoir $^{87}\text{Sr}/^{86}\text{Sr}$ is not surprising because reservoirs gather water from relatively large drainage areas which dampen effects of hydro-climatic variation on their water storage and presumably water chemistry. Thus, reservoirs integrate spatial and temporal variation present in the characteristics of their inflows. The integrative nature of reservoirs, along with our use of $^{87}\text{Sr}/^{86}\text{Sr}$ rather than elemental markers such as Sr/Ca which are known to exhibit more temporal variability (Bacon et al. 2004; Schaffler and Winkelman 2008; Walther and Thorrold 2009), likely accounts for the stability of reservoir $^{87}\text{Sr}/^{86}\text{Sr}$ signatures. The temporal stability of reservoir $^{87}\text{Sr}/^{86}\text{Sr}$ has important implications for managers. Under the right circumstances, relatively few samples, even in a single year, would be necessary to characterize the $^{87}\text{Sr}/^{86}\text{Sr}$ signature of fish in potential source reservoirs obviating the need to match known signatures from specific cohorts to unknown-history fishes (Schaffler and Winkelman 2008; Elsdon et al. 2008).

We found that $^{87}\text{Sr}/^{86}\text{Sr}$ of piscivorous species within a reservoir did not differ, with one exception. In two out of five reservoirs, $^{87}\text{Sr}/^{86}\text{Sr}$ of walleye were lower than
sympatric species. The literature does not support differential fractionation among species as a plausible explanation (Blum et al. 2000; Bentley 2006). Regardless, any possible fractionation of $^{87}\text{Sr}/^{86}\text{Sr}$ would be masked by the normalization of $^{88}\text{Sr}/^{86}\text{Sr}$ (specified value of 8.375) used in this study to correct for instrumental fractionation (Faure and Powell 1972). Reasons for the disparity are unknown but differential habitat use is likely responsible. If walleye inhabited particular areas of reservoirs not frequented by other species (e.g., the hypolimnion) and these areas differed in $^{87}\text{Sr}/^{86}\text{Sr}$ a disparity among species could arise. Dufour et al. (2007) suggested that spatial heterogeneity in $^{87}\text{Sr}/^{86}\text{Sr}$ within lakes could explain the lack of correspondence between fish remains and ambient water $^{87}\text{Sr}/^{86}\text{Sr}$. Fortunately, even in cases where walleye signatures differed from other species in the same reservoir, classification rates of individual walleye to their correct location were very high. Overall, the strong concordance of otolith $^{87}\text{Sr}/^{86}\text{Sr}$ among species within a given reservoir contributes to the utility of this marker for fingerprinting potential source locations. In general, $^{87}\text{Sr}/^{86}\text{Sr}$ signatures of suspected immigrant fish could be compared to signatures of any species from source locations, making the job of fingerprinting source locations much easier. The substitutability of species for fingerprinting sources could also alleviate the need for lethal sampling of a protected species.

While we had less opportunity to evaluate the stability of river $^{87}\text{Sr}/^{86}\text{Sr}$ since river fishes were generally of unknown provenance, $^{87}\text{Sr}/^{86}\text{Sr}$ of tagged smallmouth bass in the Yampa River had inter-annual variability comparable to reservoir temporal variability; suggesting that river $^{87}\text{Sr}/^{86}\text{Sr}$ remain stable over many years. Additionally, $^{87}\text{Sr}/^{86}\text{Sr}$ of Colorado River fishes in our study had edge signatures that were very similar to the $^{87}\text{Sr}/^{86}\text{Sr}$ of water sampled from the Colorado River near Hoover Dam (0.71075 ± 0.00003, 2σ) two decades earlier (Goldstein and Jacobsen 1987), providing further evidence that $^{87}\text{Sr}/^{86}\text{Sr}$ fluctuate little over many years in some river-reservoir systems. These findings are consistent with some other studies utilizing $^{87}\text{Sr}/^{86}\text{Sr}$ to determine the environmental history of fishes that inhabited freshwater locations. Kennedy et al. (2000) found minimal seasonal variation of $^{87}\text{Sr}/^{86}\text{Sr}$ in streams and Atlantic salmon Salmo salar otoliths from tributaries of the Connecticut River. Barnett-Johnson et al. (2008) found that $^{87}\text{Sr}/^{86}\text{Sr}$ of otoliths were similar to water $^{87}\text{Sr}/^{86}\text{Sr}$ from the same locations collected many years earlier by Ingram and Weber (1999). However, Walther and Thorrold (2009) found significant differences in $^{87}\text{Sr}/^{86}\text{Sr}$ among years of American shad Alosa sapidissima otoliths from the Hudson and Pamunkey rivers in the Eastern U.S. Nonetheless, these among-year differences explained only 5–19% of the total variability in $^{87}\text{Sr}/^{86}\text{Sr}$ detected in the two rivers. Feyrer et al. (2007) also found inter-annual differences of $^{87}\text{Sr}/^{86}\text{Sr}$, but the effect of year had little impact on discrimination of natal locations of splittail Pogonichthys macrolepidotus. While more investigation of river variability is needed in our study area, it appears that $^{87}\text{Sr}/^{86}\text{Sr}$ remain relatively stable over many years, making annual location ‘fingerprint’ updates unnecessary. Estimating the expected $^{87}\text{Sr}/^{86}\text{Sr}$ of reservoir fishes statistically allowed us to evaluate potential origins of unknown-history river-caught piscivores. Those river fish with core $^{87}\text{Sr}/^{86}\text{Sr}$ within the 95% prediction interval for a reservoir could have come from that location. Perhaps equally useful, we could use the same approach to exclude sources and thereby determine water bodies that posed lower escapement risk. However, we also showed that main stem reservoirs might have indistinguishable
$^{87}\text{Sr}/^{86}\text{Sr}$ from the river signatures immediately downstream. For example, the similarity of $^{87}\text{Sr}/^{86}\text{Sr}$ in fishes from Flaming Gorge Reservoir with $^{87}\text{Sr}/^{86}\text{Sr}$ of crayfish and age-0 (and presumably resident) smallmouth bass in river locations downstream suggests that strontium of rivers and their reservoirs upstream may not differ. Thus, at present, our approach might be most suited to situations where the emigration source is on a tributary to the river reach of interest, is in an off-channel location, or escapees are captured sufficiently downstream to be beyond the geochemical influence of the reservoir. Targeted water sampling to compare $^{87}\text{Sr}/^{86}\text{Sr}$ of reservoirs and rivers below could identify cases where signatures of reservoir and river fish would be different or the same. Additional markers (e.g., $\delta^{18}\text{O}$) could potentially improve discrimination of reservoir and river habitats and help identify reservoir escapees in rivers immediately downstream of dams. The $\delta^{2}\text{H}$ and $\delta^{18}\text{O}$ of surface waters vary predictably with latitude and elevation (Kendall and Coplen 2001), appear to differ between rivers and lakes (Henderson and Shuman 2010), and have been useful in fish provenance studies (Whitledge 2006, 2007; Walther et al. 2008).

The ambiguities we encountered in some of the known-history fish studied in the Yampa River (Figure 7) system highlight two challenges when comparing edge and core $^{87}\text{Sr}/^{86}\text{Sr}$ to infer habitat switching. First, otolith growth bands can become compressed as a fish ages, leaving a smaller amount of material deposited during that period of life. Given a fixed ablation beam diameter, spots ablated in later years of life may have less temporal resolution (here, slightly larger than 35 μm or ca. year resolution) than spots ablated closer to the core. Second, without known river-resident fish, it is difficult to infer the expected $^{87}\text{Sr}/^{86}\text{Sr}$ of a river below a reservoir source population from otoliths. Fish below dams may be permanent local residents or be recent immigrants from downstream or the reservoir upstream. The use of stationary, integrative “sentinels” of river $^{87}\text{Sr}/^{86}\text{Sr}$ could improve inference in provenance studies involving rivers and other systems where fish can move throughout heterogeneous $^{87}\text{Sr}/^{86}\text{Sr}$ environs.

Our work with crayfish carapaces and snail shells is the first we are aware of that has examined the utility of these structures as sentinels of water strontium ratio. Because $^{87}\text{Sr}/^{86}\text{Sr}$ of mudsnail shells was variable and different from other measures at the same location, we do not recommend use of this organism as a strontium sentinel. On the other hand, there was excellent correspondence of strontium ratios of crayfish carapaces, water and age-0 smallmouth bass otoliths. Strontium analysis of crayfish carapaces is a promising approach because crayfish probably integrate short term variability in the water strontium ratio as they grow. Analysis of carapaces by laser ablation is less sensitive to contamination that is problematic in solution-based analysis of water, and laser ablation was less expensive than water analyses. Crayfish gastroliths may provide an alternative structure for isotopic analysis but gastroliths are only present in crayfish at the time of molting and are thus, not readily available. Thus, future work to determine the strontium ratio at discrete locations in rivers may benefit from examination of crayfish carapaces.

The utility of natural markers to identify nonnative fish that have emigrated from reservoirs to rivers below relies upon their distinctiveness among locations and long-term temporal stability. When considering distinctness of reservoir signatures, the likelihood of overlapping $^{87}\text{Sr}/^{86}\text{Sr}$ increases as additional suspected sources are added.
Therefore, for this technique to be most effective, comparisons of otolith $^{87}\text{Sr}/^{86}\text{Sr}$ should be restricted to specific escapement hypotheses. For instance, if a suspected escapement source has been mitigated via barriers (e.g., at Rifle Gap Reservoir), subsequent sampling of river fishes downstream and analysis of $^{87}\text{Sr}/^{86}\text{Sr}$ could be performed to evaluate barrier effectiveness. Conversely, this method may be well suited to determine locations that do not appear to be sources, and thus eliminating the need of barriers or screens in those locations.

With high-resolution laser ablation MC-ICP-MS, the year of escapement may be established and could be related to environmental conditions or dam operations that may have contributed to escapement. Our findings also support the use of $^{87}\text{Sr}/^{86}\text{Sr}$ as a deterrent against illicit transfer of aquatic organisms. In a 2011 Grand County, CO criminal case $^{87}\text{Sr}/^{86}\text{Sr}$ were used to rule out source locations where a suspect was accused of illegal harvest and transportation of crayfish (B.M. Johnson, Colorado State University, unpublished data). Managers seeking to discourage illegal introductions can inform stakeholders of the forensic utility of this technology for determining provenance of aquatic organisms.

The relatively high proportion of suspected immigrant fishes captured from rivers should raise concern for managers in this region and for managers of reservoir-river systems in general. Our results suggest that efforts to control nonnative fishes in riverine critical habitat will need to continue indefinitely unless reservoir sources are contained. Because many nonnative piscivores sampled from rivers did not appear to have recruited from their location of capture, containment of reservoir sources coupled with removals in rivers may be an effective strategy to reduce the density of invasive piscivore populations. Strontium isotope ratios provide UCRB managers with the means to evaluate what reservoirs pose the greatest escapement risk and focus their control efforts most effectively.
**Literature Cited**


Wells, B.K., Reiman, B.E., Clayton, J.L., Horan, D.L., and Jones, C.M. 2003. Relationships between water, otolith, and scale chemistries of Westslope cutthroat trout from the Coeur d’Alene River, Idaho: the potential application of


Table 1. Characteristics of 15 reservoirs from which fish were sampled for otolith $^{87}\text{Sr}/^{86}\text{Sr}$. N/A = not applicable, some reservoirs were off channel. No data on hydraulic residence time available for Rio Blanco Reservoir. HRT= hydraulic residence time. CV = coefficient of variation.

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<th>Surface area (ac)</th>
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<td>0.24</td>
</tr>
<tr>
<td>Elkhead</td>
<td>ELK</td>
<td>Elkhead Cr.</td>
<td>7,028</td>
<td>899</td>
<td>24,778</td>
<td>58</td>
<td>0.48</td>
<td>0.28</td>
</tr>
<tr>
<td>Flaming Gorge</td>
<td>FGR</td>
<td>Green R.</td>
<td>6,040</td>
<td>42020</td>
<td>3,788,900</td>
<td>436</td>
<td>4.14</td>
<td>0.42</td>
</tr>
<tr>
<td>Harvey Gap</td>
<td>HGR</td>
<td>N/A</td>
<td>6,401</td>
<td>287</td>
<td>5,858</td>
<td>41</td>
<td>0.54</td>
<td>0.13</td>
</tr>
<tr>
<td>Juniata</td>
<td>JUR</td>
<td>N/A</td>
<td>5,709</td>
<td>143</td>
<td>6,868</td>
<td>54</td>
<td>1.31</td>
<td>0.05</td>
</tr>
<tr>
<td>Kenney</td>
<td>KER</td>
<td>White R.</td>
<td>5,279</td>
<td>600</td>
<td>13,800</td>
<td>71</td>
<td>0.03</td>
<td>0.31</td>
</tr>
<tr>
<td>Lake Powell</td>
<td>LKP</td>
<td>Colorado R.</td>
<td>3,614</td>
<td>160,800</td>
<td>21,505,000</td>
<td>560</td>
<td>7.20</td>
<td>--</td>
</tr>
<tr>
<td>McPhee</td>
<td>MCP</td>
<td>Dolores R.</td>
<td>6,923</td>
<td>4470</td>
<td>381,195</td>
<td>280</td>
<td>1.70</td>
<td>0.75</td>
</tr>
<tr>
<td>Paonia</td>
<td>PAO</td>
<td>N. Fork Gunnison</td>
<td>6,447</td>
<td>334</td>
<td>20,950</td>
<td>140</td>
<td>0.31</td>
<td>0.64</td>
</tr>
<tr>
<td>Red Fleet</td>
<td>RFR</td>
<td>Brush Cr.</td>
<td>5,607</td>
<td>519</td>
<td>26,020</td>
<td>144</td>
<td>1.15</td>
<td>0.60</td>
</tr>
<tr>
<td>Rifle Gap</td>
<td>RGR</td>
<td>Rifle Cr.</td>
<td>5,961</td>
<td>358</td>
<td>13,602</td>
<td>87</td>
<td>0.53</td>
<td>0.34</td>
</tr>
<tr>
<td>Rio Blanco</td>
<td>RBR</td>
<td>N/A</td>
<td>5,755</td>
<td>116</td>
<td>1,038</td>
<td>18</td>
<td>ND</td>
<td>ND</td>
</tr>
<tr>
<td>Stagecoach</td>
<td>SCR</td>
<td>Yampa R.</td>
<td>7,205</td>
<td>781</td>
<td>33,275</td>
<td>130</td>
<td>0.86</td>
<td>0.62</td>
</tr>
<tr>
<td>Starvation</td>
<td>STA</td>
<td>Strawberry R.</td>
<td>5,712</td>
<td>2760</td>
<td>162,798</td>
<td>155</td>
<td>1.53</td>
<td>0.39</td>
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Table 2. Common and scientific names and CPW taxonomic codes of fishes sampled during this study. Note that most fish are actually omnivorous so all nonnatives listed potentially could consume some life stages of fish.

<table>
<thead>
<tr>
<th>Common name</th>
<th>Scientific name</th>
<th>Code</th>
<th>Piscivore?</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black crappie</td>
<td><em>Pomoxis nigromaculatus</em></td>
<td>BCR</td>
<td>X</td>
</tr>
<tr>
<td>Bluegill</td>
<td><em>Lepomis macrochirus</em></td>
<td>BGL</td>
<td></td>
</tr>
<tr>
<td>Burbot</td>
<td><em>Lota lota</em></td>
<td>BUR</td>
<td>X</td>
</tr>
<tr>
<td>Largemouth bass</td>
<td><em>Micropterus salmoides</em></td>
<td>LMB</td>
<td>X</td>
</tr>
<tr>
<td>Northern pike</td>
<td><em>Esox lucius</em></td>
<td>NPK</td>
<td>X</td>
</tr>
<tr>
<td>Smallmouth bass</td>
<td><em>Micropterus dolomieu</em></td>
<td>SMB</td>
<td>X</td>
</tr>
<tr>
<td>Walleye</td>
<td><em>Sander vitreus</em></td>
<td>WAL</td>
<td>X</td>
</tr>
<tr>
<td>White sucker</td>
<td><em>Catostomus commersoni</em></td>
<td>WHS</td>
<td></td>
</tr>
<tr>
<td>Yellow perch</td>
<td><em>Perca flavescens</em></td>
<td>YPE</td>
<td></td>
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</tbody>
</table>
Table 3. Number of specimens of nine species of nonnative fish in the UCRB collected during 2006-2011 for microchemical analysis of otoliths and other tissues. See Table 1 for species codes. N/A indicates that that species is not known to occur in that water body, or was not targeted for sampling. Data for Lake Catamount were provided by Ryan Fitzpatrick (CPW) and Dana Winkelman (USGS CSU Coop Unit).

<table>
<thead>
<tr>
<th>Water Body</th>
<th>BCR</th>
<th>LMB</th>
<th>NPK</th>
<th>SMB</th>
<th>WAL</th>
<th>BGL</th>
<th>BUR</th>
<th>YPE</th>
<th>WHS</th>
<th>Total</th>
</tr>
</thead>
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<td>4</td>
<td>99</td>
<td>9</td>
<td>113</td>
<td>8</td>
<td>23</td>
<td>N/A</td>
<td>N/A</td>
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<td>272</td>
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<td>Crawford Reservoir (CRA)</td>
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<td>35</td>
<td>0</td>
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<td>0</td>
<td>N/A</td>
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<td>59</td>
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<td>0</td>
<td>0</td>
<td>15</td>
<td>0</td>
<td>0</td>
<td>N/A</td>
<td>N/A</td>
<td>0</td>
<td>15</td>
</tr>
<tr>
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<td>0</td>
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<td>0</td>
<td>N/A</td>
<td>N/A</td>
<td>0</td>
<td>17</td>
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<tr>
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<td>44</td>
<td>N/A</td>
<td>5</td>
<td>N/A</td>
<td>N/A</td>
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<td>110</td>
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<td>N/A</td>
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<td>0</td>
<td>N/A</td>
<td>23</td>
<td>N/A</td>
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<td>80</td>
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<td>1</td>
<td>N/A</td>
<td>N/A</td>
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<td>269</td>
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<td>Gunnison River</td>
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<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>N/A</td>
<td>0</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>Harvey Gap Res. (HGR)</td>
<td>10</td>
<td>12</td>
<td>7</td>
<td>9</td>
<td>N/A</td>
<td>3</td>
<td>N/A</td>
<td>16</td>
<td>0</td>
<td>57</td>
</tr>
<tr>
<td>Juniata Reservoir (JUR)</td>
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<td>0</td>
<td>0</td>
<td>16</td>
<td>10</td>
<td>0</td>
<td>N/A</td>
<td>0</td>
<td>0</td>
<td>26</td>
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<tr>
<td>Kenney Reservoir (KER)</td>
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<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>0</td>
<td>N/A</td>
<td>0</td>
<td>20</td>
</tr>
<tr>
<td>Lake Catamount (CAT)</td>
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<td>N/A</td>
<td>0</td>
<td>N/A</td>
<td>0</td>
<td>N/A</td>
<td>N/A</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Lake Powell (LKP)</td>
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<td>0</td>
<td>28</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>28</td>
<td></td>
</tr>
<tr>
<td>Loudy Simpson Pond (LSP)</td>
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<td>N/A</td>
<td>24</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>24</td>
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<tr>
<td>McPhee Reservoir (MCP)</td>
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<td>N/A</td>
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<td>0</td>
<td>N/A</td>
<td>0</td>
<td>0</td>
<td>42</td>
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<tr>
<td>Paonia Reservoir (PAO)</td>
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<td>N/A</td>
<td>6</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td>Red Fleet Reservoir (RFR)</td>
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<td>0</td>
<td>0</td>
<td>18</td>
<td>0</td>
<td>N/A</td>
<td>N/A</td>
<td>0</td>
<td>18</td>
</tr>
<tr>
<td>Rifle Gap Reservoir (RGR)</td>
<td>45</td>
<td>0</td>
<td>135</td>
<td>49</td>
<td>14</td>
<td>N/A</td>
<td>N/A</td>
<td>157</td>
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<td>400</td>
</tr>
<tr>
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<td>0</td>
<td>N/A</td>
<td>0</td>
<td>N/A</td>
<td>N/A</td>
<td>0</td>
<td>34</td>
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<tr>
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<td>4</td>
<td>0</td>
<td>11</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>0</td>
<td>15</td>
</tr>
<tr>
<td>Starvation Reservoir (STA)</td>
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<td>N/A</td>
<td>9</td>
<td>22</td>
<td>35</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>0</td>
<td>66</td>
</tr>
<tr>
<td>White River</td>
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<td>0</td>
<td>5</td>
<td>0</td>
<td>0</td>
<td>N/A</td>
<td>N/A</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td>Yampa River</td>
<td>39</td>
<td>0</td>
<td>56</td>
<td>181</td>
<td>1</td>
<td>57</td>
<td>N/A</td>
<td>N/A</td>
<td>21</td>
<td>355</td>
</tr>
</tbody>
</table>

| All waters              | 184 | 132 | 365 | 600 | 196 | 90  | 23  | 196 | 90  | 1884  |
Table 4. Samples from Flaming Gorge Reservoir and the Green River downstream that were analyzed for strontium ratios. “Shell” refers to New Zealand mudsnail shells, “carapace” refers to crayfish, and otoliths were from age-0 smallmouth bass. Analytical method differed depending on sample type but strontium ratios are directly comparable across analysis methods.

<table>
<thead>
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<th>Water body</th>
<th>Date</th>
<th>Sample type</th>
<th>No. collected</th>
<th>No. analyzed</th>
<th>Analysis type</th>
<th>$^{87}\text{Sr}/^{86}\text{Sr}$ Mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flaming Gorge Reservoir</td>
<td>09/13/11</td>
<td>water</td>
<td>2</td>
<td>1</td>
<td>solution</td>
<td>0.71077</td>
<td>-</td>
</tr>
<tr>
<td>Flaming Gorge Reservoir</td>
<td>05/17/07</td>
<td>otolith</td>
<td>20</td>
<td>8</td>
<td>ablation</td>
<td>0.71084</td>
<td>0.00004</td>
</tr>
<tr>
<td>Flaming Gorge Reservoir</td>
<td>09/13/11</td>
<td>carapace</td>
<td>43</td>
<td>5</td>
<td>ablation</td>
<td>0.71086</td>
<td>0.00005</td>
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<td>water</td>
<td>2</td>
<td>1</td>
<td>solution</td>
<td>0.71077</td>
<td>-</td>
</tr>
<tr>
<td>Flaming Gorge Tailwater</td>
<td>09/13/11</td>
<td>shell</td>
<td>4</td>
<td>4</td>
<td>ablation</td>
<td>0.71122</td>
<td>0.00020</td>
</tr>
<tr>
<td>Little Hole, Green River</td>
<td>09/13/11</td>
<td>water</td>
<td>2</td>
<td>1</td>
<td>solution</td>
<td>0.71075</td>
<td>-</td>
</tr>
<tr>
<td>Little Hole, Green River</td>
<td>09/13/11</td>
<td>shell</td>
<td>14</td>
<td>5</td>
<td>ablation</td>
<td>0.71088</td>
<td>0.00025</td>
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<td>water</td>
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<td>1</td>
<td>solution</td>
<td>0.71086</td>
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<td>carapace</td>
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<td>ablation</td>
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<td>ablation</td>
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<td>Canyon of Lodore</td>
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<td>11</td>
<td>ablation</td>
<td>0.71072</td>
<td>0.00018</td>
</tr>
</tbody>
</table>
Table 5. Subset of fishes collected from reservoirs in the Upper Colorado River Basin that were subjected to detailed statistical analysis to chemically fingerprint study reservoirs. Refer to Table 1 for reservoir codes and Table 2 for species codes. River codes: COR = Colorado R., DOL = Dolores R., DUC = Duchesne R., GRU = Upper Green R., WHB = White R. and YAR = Yampa R.

<table>
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<th>Water</th>
<th>Species</th>
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<th>2005</th>
<th>2006</th>
<th>2007</th>
<th>2008</th>
<th>2009</th>
<th>Total</th>
<th>Mean TL (mm)</th>
<th>Mean age (yrs)</th>
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</thead>
<tbody>
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<td>-</td>
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<td>-</td>
<td>-</td>
<td>5</td>
<td>463</td>
<td>3</td>
</tr>
<tr>
<td>CRA</td>
<td>BCR</td>
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<td>-</td>
<td>-</td>
<td>5</td>
<td>-</td>
<td>-</td>
<td>5</td>
<td>196</td>
<td>4</td>
</tr>
<tr>
<td>CRA</td>
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Mean 345 5
Table 6. Subset of fishes collected from rivers in the Upper Colorado River Basin prior to 2010 that were subjected to detailed statistical analysis to examine potential origins. Refer to Table 2 for species codes. River codes: COR = Colorado R., DOL = Dolores R., DUC = Duchesne R., GRU = Upper Green R., WHB = White R. and YAR = Yampa R.

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* Untagged, unknown history smallmouth bass
† Tagged smallmouth bass with known residence within the Yampa River
‡ Tagged smallmouth bass translocated into Elkhead Reservoir
Table 7. Walleye collected from the Green (n = 51) and Yampa rivers (n = 1) for otolith laser ablation microchemistry. RES is a reservoir (Lake Powell or Starvation), RFR is Red Fleet Reservoir, and RIV is river origin.

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<th>Location collected</th>
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<th>Wt (g)</th>
<th>Age (yr)</th>
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<th>First year in river</th>
<th>Age at river entry</th>
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Table 7. Continued. Walleye collected from the Green \((n = 51)\) and Yampa rivers \((n = 1)\) for otolith laser ablation microchemistry. RES is a reservoir (Lake Powell or Starvation), RFR is Red Fleet Reservoir, and RIV is river origin.

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</tr>
</tbody>
</table>
Table 7. Continued. Walleye collected from the Green (n = 51) and Yampa rivers (n = 1) for otolith laser ablation microchemistry. RES is a reservoir (Lake Powell or Starvation), RFR is Red Fleet Reservoir, and RIV is river origin.

<table>
<thead>
<tr>
<th>Sample No.</th>
<th>Date collected</th>
<th>Location collected</th>
<th>TL (mm)</th>
<th>Wt (g)</th>
<th>Age (yr)</th>
<th>$^{87}$Sr/$^{86}$Sr</th>
<th>First year in river</th>
<th>Age at river entry</th>
</tr>
</thead>
<tbody>
<tr>
<td>GR051507004</td>
<td>5/15/07</td>
<td>Split Mtn.-Thunder Ranch</td>
<td>537</td>
<td>1420</td>
<td>14</td>
<td>0.71009 0.71075</td>
<td>RES</td>
<td>2003</td>
</tr>
<tr>
<td>GR051507005</td>
<td>5/15/07</td>
<td>Split Mtn.-Thunder Ranch</td>
<td>438</td>
<td>905</td>
<td>4</td>
<td>0.70998 0.71137</td>
<td>RES</td>
<td>2007</td>
</tr>
<tr>
<td>GR050207001</td>
<td>5/2/07</td>
<td>Thunder Ranch</td>
<td>503</td>
<td>1275</td>
<td>13</td>
<td>0.70998 0.71074</td>
<td>RES</td>
<td>1998</td>
</tr>
<tr>
<td>GR052307001</td>
<td>5/23/07</td>
<td>Umbrella-Refuge</td>
<td>435</td>
<td>930</td>
<td>4</td>
<td>0.70992 0.71158</td>
<td>RES</td>
<td>2005</td>
</tr>
<tr>
<td>GR052406002</td>
<td>5/24/06</td>
<td>Unknown</td>
<td>410</td>
<td>670</td>
<td>3</td>
<td>0.71029 0.70997</td>
<td>RIV</td>
<td>-</td>
</tr>
<tr>
<td>GR052406003</td>
<td>5/24/06</td>
<td>Unknown</td>
<td>410</td>
<td>710</td>
<td>3</td>
<td>0.70993 0.70981</td>
<td>RES</td>
<td>2005</td>
</tr>
<tr>
<td>GR052406005</td>
<td>5/24/06</td>
<td>Unknown</td>
<td>482</td>
<td>1050</td>
<td>7</td>
<td>0.71004 0.71027</td>
<td>RES</td>
<td>2005</td>
</tr>
<tr>
<td>GR052506002</td>
<td>5/24/06</td>
<td>Unknown</td>
<td>400</td>
<td>620</td>
<td>3</td>
<td>0.70973 0.71009</td>
<td>RES</td>
<td>2006</td>
</tr>
<tr>
<td>GR052506003</td>
<td>5/24/06</td>
<td>Unknown</td>
<td>460</td>
<td>860</td>
<td>3</td>
<td>0.70974 0.71003</td>
<td>RES</td>
<td>2006</td>
</tr>
<tr>
<td>GR052506004</td>
<td>5/24/06</td>
<td>Unknown</td>
<td>425</td>
<td>700</td>
<td>2</td>
<td>0.70981 0.71000</td>
<td>RES</td>
<td>2006</td>
</tr>
<tr>
<td>GR052606003</td>
<td>5/24/06</td>
<td>Unknown</td>
<td>785</td>
<td>970</td>
<td>8</td>
<td>0.70949 0.71130</td>
<td>RES</td>
<td>2003</td>
</tr>
<tr>
<td>GR052706001</td>
<td>5/27/09</td>
<td>Unknown</td>
<td>385</td>
<td>470</td>
<td>3</td>
<td>0.70994 0.70971</td>
<td>RES</td>
<td>2006</td>
</tr>
<tr>
<td>GRUUNK09001</td>
<td>7/1/05</td>
<td>Walker Hollow</td>
<td>670</td>
<td>3315</td>
<td>10</td>
<td>0.70975 0.71046</td>
<td>RES</td>
<td>2003</td>
</tr>
<tr>
<td>YAR071610001</td>
<td>7/16/10</td>
<td>Yampa River</td>
<td>-</td>
<td>-</td>
<td>3</td>
<td>0.70967 0.71028</td>
<td>RES</td>
<td>2010</td>
</tr>
</tbody>
</table>
Table 8. Northern pike collected from the Colorado River and Redlands Fish Passage, 2011. “Mover” fish had different Sr ratio signatures in the core vs. edge, whereas “resident” fish had a constant Sr ratio throughout the otolith.

<table>
<thead>
<tr>
<th>Sample ID</th>
<th>Collection date</th>
<th>Total length (mm)</th>
<th>Wet weight (g)</th>
<th>Sex</th>
<th>Location (river mile)</th>
<th>Age (years)</th>
<th>Status</th>
<th>First year in river</th>
</tr>
</thead>
<tbody>
<tr>
<td>CO-1-1</td>
<td>07/05/11</td>
<td>680</td>
<td>1812</td>
<td>Female</td>
<td>Redlands Passage</td>
<td>3</td>
<td>Mover</td>
<td>2009</td>
</tr>
<tr>
<td>CO-1-2</td>
<td>09/26/11</td>
<td>800</td>
<td>3108</td>
<td>Male</td>
<td>186</td>
<td>4</td>
<td>Mover</td>
<td>2008</td>
</tr>
<tr>
<td>CO-1-3</td>
<td>10/18/11</td>
<td>977 head only</td>
<td></td>
<td>--</td>
<td>233.2</td>
<td>5</td>
<td>Mover</td>
<td>2007</td>
</tr>
<tr>
<td>CO-1-4</td>
<td>10/18/11</td>
<td>512</td>
<td>1003</td>
<td>Female</td>
<td>239 – 240.4</td>
<td>2</td>
<td>Resident</td>
<td>2009</td>
</tr>
<tr>
<td>CO-1-5</td>
<td>10/18/11</td>
<td>628</td>
<td>1670</td>
<td>Male</td>
<td>238 – 239</td>
<td>3</td>
<td>Resident</td>
<td>2008</td>
</tr>
<tr>
<td>CO-1-6</td>
<td>10/18/11</td>
<td>630</td>
<td>1700</td>
<td>Male</td>
<td>238.2</td>
<td>3</td>
<td>Resident</td>
<td>2008</td>
</tr>
<tr>
<td>CO-1-7</td>
<td>10/18/11</td>
<td>630</td>
<td>1835</td>
<td>Male</td>
<td>238 – 239</td>
<td>3</td>
<td>Resident</td>
<td>2008</td>
</tr>
<tr>
<td>CO-1-8</td>
<td>10/18/11</td>
<td>654</td>
<td>1893</td>
<td>Male</td>
<td>239.8</td>
<td>3</td>
<td>Resident</td>
<td>2008</td>
</tr>
<tr>
<td>CO-1-9</td>
<td>10/18/11</td>
<td>688</td>
<td>2269</td>
<td>Female</td>
<td>239 – 240.4</td>
<td>3</td>
<td>Resident</td>
<td>2008</td>
</tr>
<tr>
<td>CO-1-10</td>
<td>10/18/11</td>
<td>682</td>
<td>2302</td>
<td>Female</td>
<td>239.8</td>
<td>3</td>
<td>Resident</td>
<td>2008</td>
</tr>
</tbody>
</table>
Table 9. Sampling summary of smallmouth bass collected from Lake Powell on 04/27/2004 and used as surrogates for strontium signatures of walleyes.

<table>
<thead>
<tr>
<th>Sample ID</th>
<th>Total length (mm)</th>
<th>Weight (g)</th>
<th>Sex</th>
<th>$^{87}\text{Sr}/^{86}\text{Sr}$ Mean</th>
<th>$^{87}\text{Sr}/^{86}\text{Sr}$ SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>LP042704001</td>
<td>258</td>
<td>212</td>
<td>M</td>
<td>0.71020</td>
<td>0.00034</td>
</tr>
<tr>
<td>LP042704002</td>
<td>300</td>
<td>308</td>
<td>F</td>
<td>0.71002</td>
<td>0.00011</td>
</tr>
<tr>
<td>LP042704003</td>
<td>361</td>
<td>604</td>
<td>F</td>
<td>0.71009</td>
<td>0.00017</td>
</tr>
<tr>
<td>LP042704004</td>
<td>232</td>
<td>148</td>
<td>M</td>
<td>0.70989</td>
<td>0.00012</td>
</tr>
<tr>
<td>LP042704005</td>
<td>231</td>
<td>138</td>
<td>M</td>
<td>0.71011</td>
<td>0.00019</td>
</tr>
<tr>
<td>LP042704006</td>
<td>289</td>
<td>332</td>
<td>F</td>
<td>0.70979</td>
<td>0.00008</td>
</tr>
<tr>
<td>LP042704007</td>
<td>206</td>
<td>116</td>
<td>M</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>LP042704008</td>
<td>251</td>
<td>184</td>
<td>M</td>
<td>0.71000</td>
<td>0.00035</td>
</tr>
<tr>
<td>LP042704009</td>
<td>225</td>
<td>150</td>
<td>F</td>
<td>0.71002</td>
<td>0.00002</td>
</tr>
<tr>
<td>Mean</td>
<td>262</td>
<td>243</td>
<td>-</td>
<td>0.71000</td>
<td>-</td>
</tr>
</tbody>
</table>
Table 10. Model ranking results using Akaike’s Information Criterion for reservoir fishes. A) Analysis of random effects with a fixed intercept. Model Res × Spp × Year is for all possible combinations of species and year-specific strontium isotope ratios ($^{87}$Sr/$^{86}$Sr) in each reservoir. Model FishID is for individual fishes with multiple measures. B) Top ranked random effects model with all combinations of fixed effects reservoir (Res), species (Spp) and year. C) Dichotomous species effect (DSE; 0 = non-walleye, 1 = walleye) added in place of the all species are different effect (Spp). $\Delta_i =$ Delta $\text{AIC}_c$, $\text{ML}_i =$ Maximum Likelihood, $w_i =$ Akaike Weight and $W_{+()} =$ Cumulative Akaike Weight.

<table>
<thead>
<tr>
<th>Model</th>
<th>$\text{AIC}_c$</th>
<th>$\Delta_i$</th>
<th>$\text{ML}_i$</th>
<th>$w_i$</th>
<th>$W_{+()}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>a)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Res x Spp x Year*</td>
<td>-4524.20</td>
<td>0.00</td>
<td>1.00</td>
<td>1.00</td>
<td>-</td>
</tr>
<tr>
<td>FishID</td>
<td>-4409.60</td>
<td>114.60</td>
<td>0.00</td>
<td>0.00</td>
<td>-</td>
</tr>
<tr>
<td>b)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Res; Spp</td>
<td>-4922.60</td>
<td>0.00</td>
<td>1.00</td>
<td>0.98</td>
<td>-</td>
</tr>
<tr>
<td>Res; Spp; Year</td>
<td>-4914.90</td>
<td>7.70</td>
<td>0.02</td>
<td>0.02</td>
<td>-</td>
</tr>
<tr>
<td>Res</td>
<td>-4909.60</td>
<td>13.00</td>
<td>0.00</td>
<td>0.00</td>
<td>1.00</td>
</tr>
<tr>
<td>Res; Year</td>
<td>-4905.70</td>
<td>16.90</td>
<td>0.00</td>
<td>0.00</td>
<td>-</td>
</tr>
<tr>
<td>Spp; Year</td>
<td>-4561.20</td>
<td>361.40</td>
<td>0.00</td>
<td>0.00</td>
<td>-</td>
</tr>
<tr>
<td>Intercept</td>
<td>-4524.20</td>
<td>398.40</td>
<td>0.00</td>
<td>0.00</td>
<td>-</td>
</tr>
<tr>
<td>Spp</td>
<td>-4515.90</td>
<td>406.70</td>
<td>0.00</td>
<td>0.00</td>
<td>1.00</td>
</tr>
<tr>
<td>Year</td>
<td>-4504.10</td>
<td>418.50</td>
<td>0.00</td>
<td>0.00</td>
<td>0.02</td>
</tr>
<tr>
<td>c)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Res x DSE†</td>
<td>-4940.70</td>
<td>0.00</td>
<td>1.00</td>
<td>0.99</td>
<td>-</td>
</tr>
<tr>
<td>Res; DSE</td>
<td>-4930.30</td>
<td>10.40</td>
<td>0.01</td>
<td>0.01</td>
<td>-</td>
</tr>
</tbody>
</table>

* Model included the FishID random effect
† Model included reservoir and DSE species fixed effects
Table 11. Results from variance components analysis for each fixed effect from otolith $^{87}$Sr/$^{86}$Sr analysis.

<table>
<thead>
<tr>
<th>Fixed effects</th>
<th>FishID random effect</th>
<th>Res $\times$ Spp $\times$ Year random effect</th>
<th>Residual</th>
<th>Total variance</th>
<th>Total variance decrease (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reservoir</td>
<td>24</td>
<td>31</td>
<td>45</td>
<td>$1.22 \times 10^{-8}$</td>
<td>96</td>
</tr>
<tr>
<td>Species</td>
<td>93</td>
<td>3</td>
<td>4</td>
<td>$1.40 \times 10^{-7}$</td>
<td>50</td>
</tr>
<tr>
<td>Year</td>
<td>1</td>
<td>97</td>
<td>2</td>
<td>$2.66 \times 10^{-7}$</td>
<td>5</td>
</tr>
<tr>
<td>Intercept</td>
<td>1</td>
<td>97</td>
<td>2</td>
<td>$2.79 \times 10^{-7}$</td>
<td>-</td>
</tr>
</tbody>
</table>
Figure 1. Upper Colorado River Basin showing locations of 15 reservoirs sampled (open circles). See Table 1 for reservoir codes and names.
Figure 2. Sampling locations on the Green River where fish, water, crayfish and snails were collected for strontium analysis in September 2011.
Figure 3. Box-and-whisker plots of $^{87}\text{Sr}/^{86}\text{Sr}$ among reservoirs in six sub-basins of the Upper Colorado River Basin, including all species and years. Each box-and-whisker plot shows the distribution of $^{87}\text{Sr}/^{86}\text{Sr}$ for each individual's mean core and edge value per location. The bottom and top edges are the 25th and 75th percentiles, respectively, the middle line is the median, the diamond symbol within the box is the mean, and the whiskers contain values that are within 1.5 times the interquartile range. The number above or below each box plot is the total number of fishes ablated from each location. Refer to Table 1 for reservoir codes.
Figure 4. Summary of present best estimates of strontium isotope ratios ($^{87}\text{Sr}/^{86}\text{Sr}$) of rivers and reservoirs of the Upper Colorado River Basin. See Table 1 for reservoir names and codes.
Figure 5. Mean $^{87}\text{Sr}/^{86}\text{Sr}$ ± 2 standard errors (SE) of reservoirs in the Upper Colorado River Basin, 1999–2009. Each point on a line represents the average $^{87}\text{Sr}/^{86}\text{Sr}$ from all ablations corresponding to a given year, including all species; core and edge signatures were not averaged for each individual, since they occur in different years. Reservoirs were grouped by river sub-basin, shown in the upper part of each cell. Refer to Table 1 for reservoir names. The numbers next to each reservoir code refer to the number of fish collected and the number of species included, respectively.
Figure 6. Mean $^{87}\text{Sr}/^{86}\text{Sr} \pm 95\%$ confidence limit among species within reservoirs. Means were generated by averaging core and edge $^{87}\text{Sr}/^{86}\text{Sr}$ of each individual and then averaging these values for all individuals of a given species. Refer to Table 2 for species codes.
Figure 7. Otolith $^{87}$Sr/$^{86}$Sr profiles of smallmouth bass collected from the Yampa River, Colorado. Solid gray lines are fish that were captured from the Yampa River and translocated into Elkhead Reservoir, where they were recaptured. Black dashed lines show fish that were tagged and released within the Yampa River and had spent at least one year in the river prior to capture, 2004–2007. The dashed gray lines and triangles are untagged fish. Each fish that was tagged and relocated to Elkhead Reservoir is highlighted with an open circle. TELK refers to the number of months spent in Elkhead Reservoir after transfer to the latest otolith ablation. The gray bar represents the 95% confidence interval of the Elkhead Reservoir signature determined by predictions from the top-ranked model (analysis, phase 3).
Figure 8. Otolith $^{87}\text{Sr}/^{86}\text{Sr}$ profiles of four smallmouth bass (dashed lines) and seven walleye (solid gray lines) collected from the Colorado River, collected downstream of Rifle Gap Reservoir near Rulison, Colorado. The gray bar represents the 95% confidence interval of the Rifle Gap Reservoir signature of walleye determined by predictions from the top-ranked model (analysis, phase 3). The solid black line is the hydrograph of the Colorado River taken from US Geological Survey stream gauge station 09095500 near Cameo, Colorado, approximately 80 km downstream from Rifle Gap Reservoir.
Figure 9. Mean (8-point moving average) strontium signatures of laser ablation transects performed on otoliths of nine northern pike captured in the Colorado River and one captured at the Redlands Fish Passage on the Gunnison River (CO-1-1). The expected signatures of Rifle Gap Reservoir (RGR) and Paonia Reservoir (PAO) are not distinguishable.
Figure 10. Otolith $^{87}\text{Sr}/^{86}\text{Sr}$ profiles of five smallmouth bass (dashed lines) and 13 walleye (solid gray lines and triangle) collected from the Upper Green River, Utah. The gray bars represent the 95% confidence intervals of each reservoir signature determined by predictions from the top-ranked model (analysis, phase 3). The Starvation Reservoir bar is the modeled prediction of walleye from that reservoir. The solid black line is the hydrograph of the Strawberry River taken from US Geological Survey stream gauge station 09288180 near Duchesne, Utah, approximately 0.61 km upstream of Starvation Reservoir.
Figure 11. Strontium isotope analysis of water, otoliths, crayfish carapaces and snail shells collected in Flaming Gorge Reservoir and at four sites below Flaming Gorge Dam downstream to the Yampa River. Bars that share the same letter are not statistically different (Tukey’s Honestly Significant Difference adjustment for multiple comparisons; α = 0.05).
Figure 12. Strontium isotope ($^{87}\text{Sr}/^{86}\text{Sr}$) profiles of walleye ($n = 22$) collected from the Green River. Horizontal gray bars denote expected strontium ratio signatures for Lake Powell (LKP), Starvation (STA), and RFR (Red Fleet) reservoirs.
Figure 1. Number (black bars) and age (gray bars) of walleye (n = 42) suspected of entering the Green River from a reservoir source each year. The dashed line shows the annual hydrograph of the Strawberry River taken from U.S. Geological Survey (USGS) stream gauge station 09288180 near Duchesne, Utah, approximately 0.6 km upstream of Starvation Reservoir.
PART 2. RESERVOIR EMIGRATION RISK ASSESSMENT

Introduction
The risk of nonnative fishes emigrating downstream from reservoirs into critical habitat via entrainment in dam releases depends in general on the interplay of fish-related factors (life history, proximity, vulnerability) and reservoir-related factors (physico-chemical conditions, dam configuration, and dam operations) (Coutant and Whitney 2000; Williams et al. 2012). Fish-related factors affect entrainment risk because differences in life history will affect the life stages that are proximal to dam outlets and their behavior in flow fields, affecting their vulnerability to entrainment in surface or subsurface releases. Water conditions, dam configuration and operations will dictate spatial and temporal patterns in entrainment risk by affecting fish behavior. While considerable research has focused on downstream passage of migratory salmonids, relatively little is known about other species, particularly those of concern in the UCRB (Coutant and Whitney 2000; Williams et al. 2012). Thus, this work is somewhat hypothetical in nature. The objectives of this aspect of the project were to 1) determine how species, times, locations and dam operations affect the risk of emigration of nonnative fish from reservoirs, and 2) provide recommendations for altered dam operations, and other management measures to minimize nonnative fish emigration into critical habitat.

Methods

Fish-related Factors
To address how reproductive and developmental differences among species affect risk of emigration, we gathered basic life history information from the literature including reproductive chronology, and larval and juvenile stage growth and behavior. We determined the optimum temperature for growth and consumption for each species ($T_{opt}$), primarily from parameters of bioenergetics models for each species. We reviewed literature on how passage through dams is affected by the ecological characteristics of six predominantly piscivorous species of primary concern in the UCRB (black crappie, burbot, largemouth bass, northern pike, smallmouth bass and walleye). We assumed that fish with a higher $T_{opt}$ would locate higher in the water column during summer stratified period than fish with a lower $T_{opt}$. Thus, fishes with a higher temperature preference could be more susceptible to entrainment in surface spills, or entrainment in releases through the penstocks only when the epilimnion intersects with the penstock opening.

Reservoir Factors
Data on dam design characteristics (spillway type and elevation, elevation at top of dead pool, penstock and bypass outlet elevations and maximum normal operating depth at the dam) and operations (surface elevation, ft ASL; inflow, CFS; releases, CFS; and storage, ac-ft) were obtained from USBOR (2010) for Crawford, Flaming Gorge, McPhee, Paonia, Red Fleet, Ridgway, Rifle Gap and Starvation reservoirs. Data for non-BOR reservoirs were gathered from other agencies. Data on dam operations at Catamount and Juniata reservoirs were obtained from Colorado Division of Water Resources, for Elkhead Reservoir from the Colorado River Water Conservation District,
for Kenney Reservoir from the Rio Blanco Water Conservation District, and for Stagecoach Reservoir from the Upper Yampa Water Conservancy District. No water operations data were available for Rio Blanco Reservoir. In most cases, spills were not distinguished from other releases; thus, spills were assumed to occur when reservoir surface elevation was ≥ spillway elevation (Figure 14). Water residence time (WRT; years) was computed as:

\[
WRT = \frac{\text{CAP}}{\text{REL}}
\]

where CAP is reservoir capacity (ac-ft) and REL is total releases (ac-ft) during the period of interest.

When penstock elevation was unavailable we assumed that the penstock and top of dead pool elevations were equivalent (untrue when bypass outlets are below the main penstocks). Selective withdrawal systems (SWS) were in place at Flaming Gorge and McPhee dams so the depth of the opening to the penstocks could be manipulated by dam managers. At McPhee Dam the outflows are drawn almost exclusively from the lowest elevation outlet (SLOW #3; Anderson 2010). A series of three moveable gates covers the opening to penstocks at Flaming Gorge. Elevation of the uppermost gate was considered to be the “penstock” elevation. Daily values for these elevations and temperature profiles at Flaming Gorge Dam during 2003-2010 were obtained from D. Speas, (Reclamation, Salt Lake City, unpublished data).

We developed an index of emigration risk (ERI) for each reservoir which was the product of four dam-related emigration risk factors:

\[
\text{ERI} = \text{ST} \times \text{SL} \times \text{SF} \times \text{SD}
\]

where ST is spillway type (gated = 0.5, uncontrolled = 1.0), SL is spillway location (center = 0.5, edge = 1.0), SF is spill frequency (% of years with spills), and SD is mean spill duration (% of days of the year).

Stream flow data were gathered for streams flowing into reservoirs at the USGSa (2010) gaging station nearest each reservoir. Water year “dryness” for each reservoir’s river basin was obtained from USGSb (2010) as very dry (10th percentile), dry (10-24th percentile), normal (25-75th percentile), wet (76-90th percentile), and very wet (90th percentile). Gage and dam operations data for most reservoirs contained some invalid measurements (e.g., negative flows); these data were censored out of the dataset unless values could be estimated from preceding and succeeding values.

Results

Fish-related Factors

The nonnative species of greatest concern in the UCRB are all predominantly piscivorous, and represent four rather different Families (Centrarchidae, Esocidae, Gadidae, and Percidae) with optimum temperatures for consumption and growth ranging from the coldwater thermal guild (14 °C, burbot) to the warmwater thermal guild (29 °C, black crappie) (Table 12). These differences in thermal preference can affect the expected relative position of species in the water column during stratified conditions (Figure 15). Of the species in our study, only the burbot was expected to inhabit the
hypolimnion in summer. The other species are predicted to find water closer to their preferred temperature in the epilimnion. Most of the study reservoirs probably had maximum surface temperatures below the $T_{\text{opt}}$ of the species of concern. Thus, we would expect burbot to be most susceptible to deep releases (through hydropower penstocks or bypass outlets) in summer. The other species would likely be found higher up in the water column and more likely to be entrained in surface releases (spills) during summer. However, almost half of the reservoirs in our dataset experienced routine water level fluctuations that brought the surface to within $\leq 40$ ft of the penstock(s). At Blue Mesa Reservoir, where there are abundant temperature profile data, the epilimnion routinely extends to 40 ft (Johnson and Koski 2005). When the bottom of the epilimnion is near the penstocks the likelihood that epilimnetic species would emigrate through subsurface releases is increased.

The literature suggests that movement of non-salmonid sport fish through dams is highest during periods of high surface spills, and that these reservoir fishes might be more susceptible to entrainment during coldwater periods compared to summer (Coutant and Whitney 2000). Survival of fish would be considerably higher when entrained in surface spills than when they pass through deep outlets, particularly in dams with hydropower turbines (Coutant and Whitney 2000; Schilt 2007). However, mortality is not 100% even when fish pass through hydropower turbines, particularly for smaller fishes (Coutant and Whitney 2000). Thus, downstream emigration of all reservoir species is possible, regardless of dam configuration and water operations. Species with a proclivity to inhabit shoreline areas could be more susceptible to entrainment in spills when the spillway was located close to shore rather than in the center of the dam.

Most species had spring-summer spawning periods, but burbot spawn in winter (Table 13). The timing of the larval stage differed with species' thermal guild, but there were also significant differences in reproductive guilds. Walleye have semi-pelagic larvae and burbot have semi-pelagic eggs, while northern pike larvae are dependent upon emergent vegetation during early development. Centrarchids spawn in littoral areas and guard their eggs and larvae for weeks to months (Table 12). Thus, early life stages will experience very different emigration risk among species because their proximity to dam outlets interacts with seasons when releases typically occur.

**Reservoir Factors**

**Lake Catamount**

Lake Catamount is a quasi-privately owned, 529 ac reservoir located in Routt County, Colorado, about 5 miles south of Steamboat Springs (Table 14). The reservoir is operated by the Catamount Metropolitan District, Steamboat Springs, Colorado. The dam impounds the Yampa River, about 6 miles downstream from Stagecoach Reservoir. Lake Catamount also receives inflow from Harrison Creek. The dam had a stoplog on the spillway (Table 14) on the western end of the dam (Figure 16), and a “deep” outlet. Operations data were available from 10/26/99 to 12/31/10. There were 165 missing or censored values in spillway flow data so estimates of spill duration are underestimates. Catamount Dam spilled in every year for which we had data (Figure 17) with a mean spill duration of 196 days/year (Table 15). Hydraulic residence time (0.06; Table 1) was the second lowest in our dataset. The ERI for Lake Catamount was
0.54, the highest of the reservoirs in the study (Table 16). As presented in Part 1 of this report, emigration of nonnative fish from Lake Catamount has been detected. The reservoir houses an abundant northern pike population and rainbow trout. Colorado Division of Parks and Wildlife conducted an intensive northern pike removal during the 2000s, but current status of the northern pike population is unknown. Spills usually occurred during April-October; thus, larvae, juveniles and adults would all be present and subject to entrainment in reservoir releases over the spillway. The Catamount Metropolitan District applied for FERC approval to modify the outlet structures and install a small scale hydropower facility at the dam (DOE 2012; LCMD 2012). This construction project may present an opportunity to address the high nonnative fish emigration that is believed to occur from this reservoir by requiring emigration barriers as part of the dam renovation.

Crawford Reservoir
Crawford is a 405 ac reservoir located in Delta County, Colorado, about 28 mi southeast of Delta (Table 14), at Crawford State Park. The dam is owned by U.S. Bureau of Reclamation and is operated by the Crawford Water Conservancy District, Crawford, Colorado. The dam was completed in 1962 and it is fed by Muddy Creek, Alkali Creek, and Smith Fork Creek. The dam has an uncontrolled spillway located on the western end of the dam (Figure 18). There is also a 34 in diameter deep outlet (84 ft below surface at full pool, USBOR 2009); no structures are in place to prevent fish emigration (G. Kraai, personal communication, October 27, 2006). Operations data were available during 1990-2012. The reservoir’s surface regularly comes within ≤ 40 ft of the penstocks (mean = 64 ft; Figure 19). The reservoir spilled in 73% of years when data were available, and spill duration averaged 19 days/year, usually during April-June (Table 15). Spill duration was highest in normal to wet hydrologic years. Spills and releases can flow into Smith Fork Creek which flows into the Gunnison River; a bypass structure can also be used to release water directly into irrigation ditches. Hydraulic residence time was intermediate (0.73 years; Table 1). The ERI for Crawford Reservoir was 0.04 and it ranked 5th among the reservoirs in the study (Table 16). We did not have samples below Crawford Reservoir to know if emigration has occurred (Table 16) Nonnative sport fish present include black crappie, channel catfish, largemouth bass (one sampled in 2007; D. Kowalski, CPW, personal communication), rainbow trout, and yellow perch.

Elkhead Reservoir
This 900 ac reservoir is located on the Moffat-Routt county line about 9 mi northeast of Craig, Colorado (Table 14), at Elkhead Reservoir State Park. The reservoir is operated jointly by the City of Craig and the Colorado River Water Conservation District, Glenwood Springs, Colorado (CRWCD 2012). The dam was originally constructed in 1974 and it impounds Elkhead Creek, which empties into the Yampa River. The dam was reconfigured in 2007 to increase reservoir storage for human use and endangered fish flows, install a new spillway (ungated, on the east shore of the dam, Figure 20) and a deep release tower (77.5 ft below surface at full pool). Deep releases must pass through a ¼” aperture self-cleaning drum screen on the penstock; the spillway is unscreened. The surface remains > 40 ft above the penstock (mean depth of penstock
The reservoir spilled every year since 2007 except 2012 (Table 15; Figure 21). Average duration of spills was 43 days. Hydraulic residence time was relatively low at 0.48 years (Table 1). The ERI for Elkhead Reservoir was 0.10 and it ranked 4th (tied with Rifle Gap Reservoir) among the reservoirs in the study (Table 16). Emigration has been detected (Table 16). Smallmouth bass removed from the Yampa River were translocated to Elkhead Reservoir since 2003. Other nonnative sport fish present include black crappie, channel catfish, largemouth bass, northern pike, and rainbow trout.

Flaming Gorge Reservoir
At 42,020 ac, Flaming Gorge Reservoir (Table 14) is the largest in our dataset (excluding Lake Powell, added in last year of study). The dam is owned and operated by U.S. Bureau of Reclamation. The dam and hydropower plant were completed in 1964 and modified in 1978 and 1984. The dam impounds the Green River about 32 miles downstream from the Utah-Wyoming border at Dutch John, Utah. The dam has a gated spillway in its eastern shore (Figure 22), a 72 in diameter unscreened bypass outlet below 200 ft, and three selective withdrawal structures (SWS) that cycle between about 40 ft deep in summer to 110 ft deep in winter (Figure 23). Hydraulic residence time was high (4.14 years; Table 1). Besides brief annual tests of the spillway, the dam has spilled only three times since 1983: in 1983, 1997, and 1999. The ERI for Flaming Gorge Reservoir was < 0.01, placing it at the bottom of the list (tied with McPhee and Red Fleet reservoirs) (Table 16). As discussed in Part 1 of this report, we were unable to distinguish reservoir signatures from signatures of the Green River so emigration from Flaming Gorge is unknown at this time. Fish remains have not been observed in annual inspections of the power plant (R. Clayton, BOR, personal communication, February 20, 2007). The bypass tubes are used occasionally to enhance river flow and withdrawals through the SWS in April-October are epilimnetic to release warmer water into the river. Water temperature at the level of the SWS opening was about 4 °C in winter to as high as 18 °C in summer (Figure 23). Temperature at the outlet corresponded most closely with the optimum temperature for burbot suggesting that this species could be more likely to be entrained in outflows than others. Nonnative sport fish present include burbot, channel catfish, kokanee, smallmouth bass, and lake trout, rainbow trout and brown trout.

Harvey Gap Reservoir
Also called Grass Valley Reservoir, 287 ac Harvey Gap Reservoir (Table 14) is located in Garfield County, Colorado, about 5 miles north of the town of Silt, at Harvey Gap State Park. The reservoir is operated by Silt Water Conservancy District (SWCD), Silt, Colorado. The reservoir receives water via transfers from Rifle Creek above Rifle Gap Reservoir via the Grass Valley Canal (Figure 24). The reservoir does not spill, it is used only for storage of irrigation water (W. West, SWC, personal communication, October 6, 2006). Hydraulic residence time was intermediate (0.54 years; Table 1). We did not have information on the outlet configuration, but we did not include Harvey Gap Reservoir in our emigration risk index because it does not have an outlet leading directly to critical habitat. However, several nonnative sport fish are present including black crappie, channel catfish, largemouth bass, northern pike, smallmouth bass, trout, and
yellow perch. Thus, the reservoir is a source for unauthorized transfers of nonnative fish to critical habitat.

**Juniata Reservoir**

Juniata Reservoir is located about 15 mi southeast of the City of Grand Junction, Colorado. The reservoir is managed by the City of Grand Junction for its municipal use. At 143 ac at full pool, it is the second smallest reservoir in our dataset (Table 14). The dam has a selective withdrawal system allowing managers to choose the depth of withdrawals which are sent to Grand Junction via a pipeline. The reservoir is filled with water from Kannah Creek, a ditch, and the North Fork of Kannah Creek. The reservoir releases and spills irregularly into Hallenbeck Reservoir (Figure 25) which drains to the Gunnison River via Kannah Creek. Hydraulic residence time was high (1.31 years, Table 1). We did not include Juniata Reservoir in our emigration risk index. However, several nonnative sport fish are present including large- and smallmouth bass, trout, and walleye. Thus, the reservoir is a source for unauthorized transfers of nonnative fish to critical habitat.

**Kenney Reservoir**

Also known as Taylor Draw Reservoir, this 600 ac reservoir (Table 14) is located about 5 mi east of Rangely, Colorado. The dam was completed in 1984 and it is operated by the Rio Blanco Water Conservancy District, Rangely, Colorado. The dam impounds the White River which flows into the Green River. There is an uncontrolled spillway in the center of the dam (Figure 26), a bypass tube and penstock for hydropower generation. It is believed that small fish could survive passage through the power plant (D. Eddy, RBWCD, personal communication, January 4, 2007). Operations data were available for January 2003 to December 2006. The dam spills every spring for an average of 188 days (Table 15; Figure 27) and hydraulic residence time was the lowest in our dataset (0.03 years; Table 1). The ERI for Kenney Reservoir was 0.26, the second highest of the reservoirs in the study (Table 16). As discussed in Part 1 of this report, we were unable to distinguish reservoir signatures from signatures of the White River so emigration from Kenney Reservoir is unknown at this time. Nonnative sport fish present include black crappie, channel catfish and rainbow trout.

**McPhee Reservoir**

This 4,470 ac reservoir (Table 14) is located in Montezuma County, near Dolores, Colorado. McPhee is the second largest reservoir in our dataset. The dam and power plant are owned by U.S. Bureau of Reclamation. The dam is operated by Dolores Water Conservancy District (DWCD), Cortez, Colorado. The dam includes hydropower turbines, and was constructed in 1984 and it impounds the Dolores River which empties into the Colorado River. The outlet works consist of 3 selective withdrawal levels (upper two are almost never used, Anderson 2010), a bypass outlet, and a gated spillway on the northwestern side of the dam (Figure 28) that is no longer used. The reservoir’s surface regularly comes within ≤ 40 ft of the penstocks (Figure 29) but the spillway has not been used since 1996. Hydraulic residence time was high (1.7 years, Table 1). Primarily because it very rarely spills, McPhee Reservoir was at the bottom of the emigration risk index (ERI < 0.01), tied with Flaming Gorge and Red Fleet reservoirs. As
discussed in Part 1 of this report, we were unable to distinguish reservoir signatures from downstream river signatures so emigration from McPhee Reservoir is unknown at this time. Nonnative sport fish present include black crappie, channel catfish, kokanee, largemouth bass, northern pike, rainbow trout, walleye and yellow perch.

**Paonia Reservoir**
This 334 ac reservoir (Table 14) is located in Delta County, about 13 miles northeast of Paonia, Colorado. The dam is owned by the U.S. Bureau of Reclamation and is operated by North Fork Water Conservancy (NFWC), Hotchkiss, Colorado. The reservoir is also the site of Paonia State Park. The dam was completed in 1962 and it impounds Muddy Creek, which then flows into the North Fork of the Gunnison River. The spillway is located on the north end of the dam (Figure 30). The reservoir’s surface regularly comes within < 40 ft and often within < 20 ft of the penstocks (Figure 31). The reservoir spilled in 20 of 20 (100%) years when data were available, and spill duration averaged 58 days/year (Table 15). In general, spill duration was highest in normal to wet hydrologic years. Hydraulic residence time was low (0.31 years, Table 1). The ERI for Paonia Reservoir was 0.16, the third highest of the reservoirs in the study (Table 16). We did not have samples of river fish from below Paonia Reservoir to determine if emigration had occurred (Table 16). However, no fish exclusion structures are used on releases. The dam tender stated observing northern pike leaving the reservoir (M. Denison, NFWC, personal communication, November 11, 2006). Nonnative sport fish present included northern pike and rainbow trout. In 2012 the reservoir was chemically treated to remove northern pike.

**Red Fleet Reservoir**
This 1,285 ac reservoir (Table 14) is located about 10 miles northeast of Vernal, Utah, within Red Fleet State Park. The dam is owned by the U.S. Bureau of Reclamation and is operated by Uintah Water Conservancy District, Vernal, Utah. The dam was completed in 1980 and it impounds Big Brush Creek which flows into the Green River. The water surface remains > 40 ft above the penstocks (mean = 82 ft). The spillway is located on the east end of the dam (Figure 32). The reservoir spilled in 7 of 20 (33%) years when data were available, and spill duration averaged 3 days/year (Table 15). Spill duration was positively correlated with hydrologic conditions, with normal to wet years usually having the longest period of spills (with the exception of 2001) (Figure 33). Hydraulic residence time was high (1.15 years, Table 1). The ERI for Red Fleet Reservoir (<0.01) was second lowest in the set of the reservoirs in the study (Table 16). Despite its low risk index, we believe we detected walleye emigration from Red Fleet Reservoir (see Part 1 of this report). Nonnative sport fish present include largemouth bass, sunfish, rainbow trout and walleye.

**Ridgway Reservoir**
This 1,030 ac reservoir (Table 14) is located within Ridgway State Park, about 3 miles north of Ridgway, Colorado. The dam is owned by the U.S. Bureau of Reclamation and is operated by Tri-County Water Conservancy District (TCWCD), Montrose, Colorado. The dam was completed in 1987 and it impounds the Uncompahgre River which then flows into the Gunnison River. The outlet works consist of an uncontrolled morning glory
spillway on the east side of the dam (Figure 34), a bypass tube, and penstocks conveying water back to the river. No structures are in place to prevent fish emigration (M. Berry, TCWCD, personal communication, October 16, 2006). The water surface remains >40 ft above the penstocks (mean = 136 ft) (Figure 35). The reservoir spilled in 7 of 20 (35%) years when data were available, and spill duration averaged 7 days/year (Table 15). Spill duration was not correlated with hydrologic conditions in the drainage, with the longest spills in 1990-1991 when hydrologic conditions in the drainage were dry. Hydraulic residence time was intermediate (0.59 years, Table 1). The ERI for Ridgway Reservoir was 0.01, among the lowest of the reservoirs in the study (Table 16). No samples from downstream of the dam were available (Table 16). Nonnative sport fish present include kokanee, largemouth bass, rainbow and brown trout, and yellow perch.

**Rifle Gap Reservoir**

This 358 ac reservoir Table 14) is located about 6 miles north of Rifle, Colorado in Rifle Gap State Park. The dam is owned by U.S. Bureau of Reclamation and is operated by Silt Water Conservancy District (SWCD), Silt, Colorado. The dam was completed in 1967 and impounds East, Middle and West Rifle Creeks; its releases flow into the Colorado River. The spillway is located on the eastern end of the dam (Figure 36). The reservoir spilled in 12 of 17 (71%) years when data were available (Table 15). Since 1994 RGR has spilled an average of 79 d/year. Spill duration was higher in the 1990s (109 d/year) than in the 2000s (49 d/year), and was > 100 d in 1996, 1998 and 1999 (Figure 37). Spill duration was highest in April and was higher during January-July than during August-December. The reservoir usually only spilled during normal to wet hydrologic years but there was a number of years without data. Spill duration was more than 100% higher during 1990s than during the 2000s. The reservoir’s surface regularly came within ≤ 40 ft of the penstocks (Figure 37). No fish exclusion structures were used on releases (W. West, SWC, personal communication, October 6, 2006) but a barrier on Rifle Creek below the dam was recently installed. Hydraulic residence time was intermediate (0.53 years, Table 1). The ERI for Rifle Gap Reservoir was intermediate (ERI = 0.10) and tied with Elkhead Reservoir (Table 16). As presented in Part 1 of this report, we found strong evidence for emigration of walleye and northern pike from Rifle Gap Reservoir to the Colorado River. Nonnative sport fish present include black crappie, largemouth bass, northern pike, smallmouth bass, rainbow and brown trout, walleye, and yellow perch.

**Rio Blanco Reservoir**

Rio Blanco Reservoir (116 ac; Table 14) is located about 16 mi northeast of Meeker, Colorado in Rio Blanco State Wildlife Area. The reservoir is an off channel reservoir along the White River (Figure 38), with the smallest surface area and mean depth in our reservoir dataset (Table 1). Rio Blanco Reservoir is filled by an inlet on the White River and an irrigation ditch. An exclusion device was constructed on the inlet in the late 1980s to prevent northern pike from entering the White River from the reservoir. The dam releases into the White River. The dam has a fixed stop log outlet structure and an uncontrolled 24 inch penstock passing through the dam (C. Wood, CPW, personal communication, January 4, 2007). No operations data were available for this reservoir
so hydraulic residence time and ERI could not be computed. Anecdotal information indicated that the reservoir rarely spills (C. Wood, CPW, personal communication, January 4, 2007). No samples from below the reservoir were available (see Part 1). Nonnative sport fish present include black crappie, bluegill, channel catfish, largemouth bass, northern pike, smallmouth bass, and yellow perch.

**Stagecoach Reservoir**

This 781 ac reservoir (Table 14) is located within Stagecoach State Park, about 4 mi east of Oak Creek, Colorado. The dam is owned by and operated by Upper Yampa Water Conservancy District (UYWCD), Steamboat Springs, Colorado for storage and hydropower generation. The dam was completed in 1989 and it impounds the Yampa River, which then flows into Lake Catamount. Water can be released via an uncontrolled spillway in the center of the dam (Figure 39), and via a multi-port outlet structure. Operations data were available during 1989-2005. The reservoir’s surface remained > 40 ft above the deep outlet (mean = 64 ft); the dam spilled in 11% of years for a mean duration of 74 days, usually during May-August (Table 15). Spills were most prolonged (>75 days/year) in 1995-1999 (Figure 40). Hydraulic residence time was intermediate (0.86 years, Table 1). The ERI for Stagecoach Reservoir was relatively low (0.01), tied with Ridgway Reservoir (Table 16). We did not have any fish samples from below Stagecoach Reservoir (and above Lake Catamount) to evaluate if emigration had occurred (Table 16). Nonnative sport fish present include northern pike, rainbow trout, and walleye.

**Starvation Reservoir**

This 3,310 ac reservoir (Table 14) is located within Starvation State Park, about 3 mi west of Duchesne, Utah. The dam is owned by U.S. Bureau of Reclamation and is operated by Central Utah Water Conservancy District, Orem, Utah. The reservoir is the water supply for the city of Duchesne. The dam was completed in 1967, impounding the Strawberry River which flows into the Duchesne River before reaching the Green River. Water can also be added from diversions on the Duchesne River. The spillway is located on the western end of the dam (Figure 41). The water surface remains > 40 ft above the penstocks (mean = 106 ft; Figure 42). The reservoir is operated to spill annually (Brunson et al. 2007), and it did so in 15 of 21 (71%) years when data were available. Spill duration averaged 21 days/year (Table 15). Unlike most of the other reservoirs in our study, spill duration at Starvation Reservoir was not well correlated with hydrologic conditions in the drainage (Figure 42). Hydraulic residence time was high (1.53 years, Table 1). The ERI for Starvation Reservoir was intermediate (0.04) and tied with Ridgway Reservoir (Table 16). Nonnative sport fish present include smallmouth bass, rainbow trout, walleye, and yellow perch. A study of fish escapement conducted during 2002-2005 (Brunson et al. 2007) detected escapement of walleye, smallmouth bass, yellow perch and salmonids. We found isotopic evidence that walleye had likely emigrated from the reservoir (see Part 1, this report).

**Discussion**

Examination of fish-related factors showed that emigration risk of early life stages differed among species. Young walleye and burbot should have the highest likelihood of
emigrating downstream because they have semi-pelagic eggs and larvae and they exhibit no parental care, and survival of early life stages passing through dams should be high. Northern pike are the earliest spring spawners, suggesting high emigration risk of early life stages in March-May releases, but they spawn and the larvae develop on wetland vegetation, usually rare in the vicinity of dams. Centrarchids spawn later than the other three species, and they all exhibit some degree of parental care. Thus, emigration of young centrarchids would be of no consequence until juveniles no longer require parental care, in mid- to late summer. The literature suggests that movement of non-salmonids past dams is highly episodic and variable across species (Coutant and Whitney 2000). However, movement and survival of adults of many non-salmonid species is greatest during periods of high releases over spillways. Survival of fish passed in surface spills can be greater than 90% but even passage through hydropower turbines does not induce complete mortality (Coutant and Whitney 2000; Schilt 2007). Thus, while knowledge of downstream movement of non-migratory fish is weak (Williams et al. 2012), behavior and life history factors that place fish in the proximity of either surface or subsurface releases can result in successful downstream emigration.

The majority of the dams in our study were configured and operated in a manner that allows for downstream emigration of nonnative sport fish. In half of the reservoirs (Crawford, Flaming Gorge, McPhee, Paonia, Rifle Gap reservoirs) the penstocks were < 40 ft below the surface at all times, increasing the risk of emigration of epilimnetic species through the penstocks. At Elkhead, Red Fleet, Ridgway, Stagecoach, and Starvation reservoirs the penstocks remained >40 ft below the surface (as of 2010). This probably reduced the likelihood of emigration through the penstocks. However, it is reasonable to expect that all the reservoirs in the region will experience greater drawdowns associated with climate change and increasing water demand, and thus a higher risk of penstock entrainment in the future.

Most reservoirs had dam spillways that were unscreened contributing to higher risk of emigration over the spillway. Most spillways were also located on a shoreline end (edge) of the dam. We would expect littoral zone species (most nonnative sport fish in UCRB) would be more susceptible to entrainment in surface releases from such spillways. All of the reservoirs for which we had data (n=12) spilled, but at different frequencies and durations. In general, spill frequency and duration were positively correlated (r = 0.59). More than half of the reservoirs spilled in ≥ 50% of years for an average of 82 days per year. Spills occurred in different months among reservoirs, but all had spills during the month of June. Spills were not always correlated with hydrologic conditions- spills occurred in several reservoirs even during dry climate periods. Thus, predicting when spills and associated fish emigration might occur is difficult. On the basis of spillway configuration, and spill frequency and duration, we estimated that Catamount, Kenney, Elkhead, Rifle Gap reservoirs could have the highest likelihood of fish emigration. However, we found evidence that emigration had occurred from most of the reservoirs with uncontrolled/unscreened spillways, regardless of spill frequency or duration.

The longer that dams lack structures limiting downstream emigration, and spill frequently, the more fish emigration to critical habitat contributes to propagule pressure and increases the likelihood that more species will become established below dams. Given the prevalence of fish emigration from reservoirs, stocking of new nonnative
species, by agencies and the public, should be discouraged. Until more is known about factors driving nonnative fish movement past dams, altered dam operations that 1) minimize spills and 2) keep the reservoir surface as far from penstocks as practical may be the most pragmatic approach to minimizing downstream emigration of nonnative sport fish.

Conclusions
- Behavior and life history characteristics that place fish in the proximity of either surface or subsurface releases can result in successful downstream emigration.
- Walleye and burbot may be more susceptible to downstream emigration than the other nonnative species in systems with predominantly sub-surface releases and spillways in the center of dams.
- Survival and likelihood of downstream emigration of most species was probably higher in reservoirs that spilled frequently.
- The majority of dams in our study were configured and operated in a manner that allows for downstream emigration of nonnative sport fish
- Only two reservoirs (Kenney and Stagecoach) had spillways located in the center of the dam. The remainder of spillways were located adjacent to the shore, with a higher likelihood of entrainment of littoral zone oriented species.
- Most of the reservoirs spilled; over half of them (7/12) spilled in at least 50% of years. Reservoirs with the highest spill frequencies were usually also the ones where fish emigration was detected.
- About 60% of reservoirs spilled every other year or more and nonnative fish emigration has been detected directly by sampling or indirectly from otolith signatures in most of them.
Literature Cited


Table 12. Reproductive ecology and optimum temperature ($T_{opt}$, adults) of nonnative fishes in Upper Colorado River Basin reservoirs. Sources for ecological information are referenced in footnotes.

<table>
<thead>
<tr>
<th>Species</th>
<th>Spawning Season</th>
<th>Initiation ($^\circ$C)</th>
<th>Peak ($^\circ$C)</th>
<th>Depth eggs laid (m)</th>
<th>Incubation time (d or GDD)</th>
<th>Size at hatching (mm)</th>
<th>Larval behavior</th>
<th>Adult $T_{opt}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black crappie</td>
<td>Late spring</td>
<td>14.4$^a$</td>
<td>19.5$^{ac}$</td>
<td>0.25 to &gt;2$^c$</td>
<td>3-5 d$^c$</td>
<td>“minute”$^c$</td>
<td>Guarded until first feeding$^c$</td>
<td>29 $^e$</td>
</tr>
<tr>
<td>Burbot</td>
<td>Winter$^c$</td>
<td>Dec-Mar$^d$ ($surface$)$^c$</td>
<td>&lt;3$^c$</td>
<td>60-120 d$^d$</td>
<td>3.5$^b$</td>
<td>no parental care, semi-pelagic eggs$^c$</td>
<td>14 $^h$</td>
<td></td>
</tr>
<tr>
<td>Largemouth bass</td>
<td>Early summer$^c$</td>
<td>15.6$^a$</td>
<td>18.3$^a$</td>
<td>0.6$^a$</td>
<td>3-4 d$^d$</td>
<td>3$^c$</td>
<td>Male guards for at least one month, then independent (30 mm)$^d$</td>
<td>27 $^f$</td>
</tr>
<tr>
<td>Northern pike</td>
<td>Early spring$^c$</td>
<td>2.2-2.8 (spawning migration)$^a$</td>
<td>7.8$^c$</td>
<td>0.2$^a$</td>
<td>210-270 DD above 32$^o$F$^a$</td>
<td>7$^c$</td>
<td>Emigrate from wetlands at 20 mm (18-24 d after hatch)$^c$</td>
<td>24 $^e$</td>
</tr>
<tr>
<td>Smallmouth bass</td>
<td>Early summer$^c$</td>
<td>15 (nest construction)$^a$</td>
<td>17$^c$</td>
<td>0.4-3.7$^a$</td>
<td>2.2-2.5$^d$</td>
<td>Larvae guarded 14 d$^d$</td>
<td></td>
<td>22 $^g$</td>
</tr>
<tr>
<td>Walleye</td>
<td>Spring$^c$</td>
<td>3.3-6.7 (spawning migration)$^a$</td>
<td>5.6-10$^a$</td>
<td>&lt;1.0$^a$</td>
<td>4.4$^c$: 26d, 11.5$^c$: 21d, 13.9$^c$: 7$^d$</td>
<td>7.3$^c$</td>
<td>Pelagic until 25-30 mm, then move inshore$^c$</td>
<td>22 $^e$</td>
</tr>
</tbody>
</table>

Table 13. Approximate reproductive chronology of nonnative sport fish in reservoirs of the Upper Colorado River Basin. Light gray boxes indicate period of spawning, incubation and parental care; medium gray boxes indicate period when larvae are independent; and dark gray boxes indicate the period of juvenile growth of each species.

<table>
<thead>
<tr>
<th>Species</th>
<th>JAN</th>
<th>FEB</th>
<th>MAR</th>
<th>APR</th>
<th>MAY</th>
<th>JUN</th>
<th>JUL</th>
<th>AUG</th>
<th>SEP</th>
<th>OCT</th>
<th>NOV</th>
<th>DEC</th>
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<tbody>
<tr>
<td>BUR</td>
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<td>LMB</td>
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<tr>
<td>BCR</td>
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<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
</tbody>
</table>
Table 14. Characteristics of study reservoirs at full pool (NA = not present or not used, ND = no data). If penstock/outlet elevation was not reported then it was assumed to be top of dead storage.

<table>
<thead>
<tr>
<th>Reservoir</th>
<th>Code</th>
<th>Surface area (ac; full pool)</th>
<th>Normal surface elevation (ft)</th>
<th>Spillway crest (ft)</th>
<th>Normal max. depth at dam (ft)</th>
<th>Depth of penstock (ft)</th>
<th>Penstock elevation (ft)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Catamount</td>
<td>CAT</td>
<td>529</td>
<td>ND</td>
<td>6,915.0</td>
<td>ND</td>
<td>ND</td>
<td>6,866.0</td>
</tr>
<tr>
<td>Crawford</td>
<td>CRA</td>
<td>405d</td>
<td>6,553d</td>
<td>6,553.3</td>
<td>144.0d</td>
<td>84.0</td>
<td>ND</td>
</tr>
<tr>
<td>Elkhead</td>
<td>ELK</td>
<td>900f</td>
<td>6,388e</td>
<td>6,388.0</td>
<td>58.1</td>
<td>ND</td>
<td>6,310.5</td>
</tr>
<tr>
<td>Flaming Gorge</td>
<td>FGR</td>
<td>42,020d</td>
<td>6,040d</td>
<td>6,046.0</td>
<td>453.0d</td>
<td>SW</td>
<td>5,850.0</td>
</tr>
<tr>
<td>Harvey Gap</td>
<td>HGR</td>
<td>287a</td>
<td>6,402</td>
<td>NA</td>
<td>41.0</td>
<td>ND</td>
<td>ND</td>
</tr>
<tr>
<td>Juniata</td>
<td>JUR</td>
<td>143</td>
<td>5,709</td>
<td>5,740.4</td>
<td>54.1</td>
<td>ND</td>
<td>5,605a</td>
</tr>
<tr>
<td>Kenney</td>
<td>KER</td>
<td>600</td>
<td>5,280</td>
<td>5,303.5</td>
<td>71.0</td>
<td>ND</td>
<td>ND</td>
</tr>
<tr>
<td>McPhee</td>
<td>MCP</td>
<td>4,470d</td>
<td>6,924d</td>
<td>6,897.0</td>
<td>262.0d</td>
<td>248.0</td>
<td>6720.0</td>
</tr>
<tr>
<td>Paonia</td>
<td>PAO</td>
<td>334d</td>
<td>6,447d</td>
<td>6,447.5</td>
<td>167.0d</td>
<td>89.0</td>
<td>6,358.0</td>
</tr>
<tr>
<td>Red Fleet</td>
<td>RFR</td>
<td>1,285</td>
<td>5,560.7d</td>
<td>5,608.2</td>
<td>138.0d</td>
<td>102.0</td>
<td>5,506.0</td>
</tr>
<tr>
<td>Ridgway</td>
<td>RWR</td>
<td>1,030</td>
<td>6871d</td>
<td>6,871.3</td>
<td>200.0d</td>
<td>151.1</td>
<td>6,741.0</td>
</tr>
<tr>
<td>Rifle Gap</td>
<td>RGR</td>
<td>358d</td>
<td>5,960d</td>
<td>5,960.0</td>
<td>113.8d</td>
<td>57.0</td>
<td>5,903.0</td>
</tr>
<tr>
<td>Rio Blanco</td>
<td>RBR</td>
<td>116</td>
<td>5,756</td>
<td>ND</td>
<td>18.0</td>
<td>ND</td>
<td>ND</td>
</tr>
<tr>
<td>Stagecoach</td>
<td>SCR</td>
<td>781</td>
<td>7205d</td>
<td>7,200.0</td>
<td>129.9</td>
<td>74.0</td>
<td>7,131.0</td>
</tr>
<tr>
<td>Starvation</td>
<td>STA</td>
<td>3,310g</td>
<td>5,712d</td>
<td>5,712.0</td>
<td>162.0d</td>
<td>117.0g</td>
<td>5,595.0</td>
</tr>
</tbody>
</table>

Table 15. Annual spill frequency and duration (days/yr), and minimum penstock depth (computed from daily reservoir elevations) of mainstem dams and reservoir emigration status. Data on spill frequency was not available for most reservoirs. Thus, reservoirs were assumed to spill if surface elevation ≥ spillway elevation. UC = uncontrolled crest, GS = gated spillway, MG = morning glory, SL = stop log, SW = selective withdrawal, NA = not present/not used, ND = no data.

<table>
<thead>
<tr>
<th>Reservoir</th>
<th>Data period</th>
<th>Spillway type</th>
<th>Spillway location</th>
<th>Spill frequency</th>
<th>Mean spill duration</th>
<th>Typical period of spills</th>
<th>Minimum penstock depth (ft)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Catamount*</td>
<td>1999-2010</td>
<td>SL</td>
<td>Edge</td>
<td>1.00</td>
<td>196</td>
<td>Apr-Oct</td>
<td>ND</td>
</tr>
<tr>
<td>Crawford</td>
<td>2004-2012</td>
<td>UC</td>
<td>Edge</td>
<td>0.73</td>
<td>19</td>
<td>Apr-Jun</td>
<td>≤ 40</td>
</tr>
<tr>
<td>Elkhead**</td>
<td>2007-2012</td>
<td>UC</td>
<td>Edge</td>
<td>0.83</td>
<td>43</td>
<td>Apr-Jul</td>
<td>&gt; 40</td>
</tr>
<tr>
<td>Flaming Gorge</td>
<td>1983-2010</td>
<td>GS</td>
<td>Edge</td>
<td>0.07</td>
<td>20</td>
<td>Jun</td>
<td>≤ 40</td>
</tr>
<tr>
<td>Kenney</td>
<td>2003-2006</td>
<td>UC</td>
<td>Center</td>
<td>1.00</td>
<td>188</td>
<td>Mar-Dec</td>
<td>ND</td>
</tr>
<tr>
<td>McPhee</td>
<td>1990-2010</td>
<td>GS</td>
<td>Edge</td>
<td>0.05</td>
<td>9</td>
<td>Jun</td>
<td>≤ 40</td>
</tr>
<tr>
<td>Paonia</td>
<td>1990-2010</td>
<td>UC</td>
<td>Edge</td>
<td>1.00</td>
<td>58</td>
<td>May-Jul</td>
<td>≤ 40</td>
</tr>
<tr>
<td>Red Fleet</td>
<td>1990-2010</td>
<td>UC</td>
<td>Edge</td>
<td>0.33</td>
<td>3</td>
<td>Jun</td>
<td>&gt; 40</td>
</tr>
<tr>
<td>Ridgway</td>
<td>1990-2010</td>
<td>UC, MG</td>
<td>Edge</td>
<td>0.40</td>
<td>7</td>
<td>May-Jun</td>
<td>&gt; 40</td>
</tr>
<tr>
<td>Rifle Gap</td>
<td>1994-2010</td>
<td>UC</td>
<td>Edge</td>
<td>0.80</td>
<td>47</td>
<td>Feb-Jul†</td>
<td>≤ 40</td>
</tr>
<tr>
<td>Stagecoach</td>
<td>1989-2005</td>
<td>UC</td>
<td>Center</td>
<td>0.11</td>
<td>74</td>
<td>May-Aug</td>
<td>&gt; 40</td>
</tr>
<tr>
<td>Starvation</td>
<td>1990-2010</td>
<td>UC</td>
<td>Edge</td>
<td>0.71</td>
<td>21</td>
<td>Jun-Jul</td>
<td>&gt; 40</td>
</tr>
</tbody>
</table>

*2000-2010
**post-expansion, April 2007- September 2012
†Spill months highly variable
Table 16. Spillway related emigration risk factors and overall emigration risk index at 12 reservoirs in the Upper Colorado River basin. Emigration risk index was the product of the four risk factors. See text for details. Detection of emigration based on core and edge $^{87}\text{Sr}/^{86}\text{Sr}$ (Sr), recaptures of tagged fish (tags), or sampling of outflows (sampling). NS = no samples; NK = not known since reservoir and downstream river were not distinguishable.

<table>
<thead>
<tr>
<th>Reservoir</th>
<th>Spillway type</th>
<th>Spillway location</th>
<th>Spill frequency</th>
<th>Mean spill duration</th>
<th>Emigration risk index</th>
<th>Emigration rank</th>
<th>Emigration detected?</th>
<th>Detection method</th>
</tr>
</thead>
<tbody>
<tr>
<td>Catamount*</td>
<td>1.0</td>
<td>1.0</td>
<td>1.00</td>
<td>0.54</td>
<td>0.54</td>
<td>1</td>
<td>YES</td>
<td>Sr, tags</td>
</tr>
<tr>
<td>Kenney</td>
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<td>0.5</td>
<td>1.00</td>
<td>0.52</td>
<td>0.26</td>
<td>2</td>
<td>NK</td>
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<tr>
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<td>1.00</td>
<td>0.16</td>
<td>0.16</td>
<td>3</td>
<td>NS</td>
<td>--</td>
</tr>
<tr>
<td>Elkhead**</td>
<td>1.0</td>
<td>1.0</td>
<td>0.83</td>
<td>0.12</td>
<td>0.10</td>
<td>4</td>
<td>YES</td>
<td>Sr, tags</td>
</tr>
<tr>
<td>Rifle Gap</td>
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<td>1.0</td>
<td>0.80</td>
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<td>0.10</td>
<td>4</td>
<td>YES</td>
<td>Sr</td>
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<tr>
<td>Crawford</td>
<td>1.0</td>
<td>1.0</td>
<td>0.73</td>
<td>0.05</td>
<td>0.04</td>
<td>5</td>
<td>NS</td>
<td>--</td>
</tr>
<tr>
<td>Starvation</td>
<td>1.0</td>
<td>1.0</td>
<td>0.71</td>
<td>0.06</td>
<td>0.04</td>
<td>5</td>
<td>YES</td>
<td>Sr, sampling</td>
</tr>
<tr>
<td>Ridgway</td>
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<td>1.0</td>
<td>0.40</td>
<td>0.02</td>
<td>0.01</td>
<td>6</td>
<td>NS</td>
<td>--</td>
</tr>
<tr>
<td>Stagecoach</td>
<td>1.0</td>
<td>0.5</td>
<td>0.11</td>
<td>0.20</td>
<td>0.01</td>
<td>6</td>
<td>NS</td>
<td>--</td>
</tr>
<tr>
<td>Flaming Gorge</td>
<td>0.5</td>
<td>1.0</td>
<td>0.07</td>
<td>0.05</td>
<td>&lt; 0.01</td>
<td>7</td>
<td>NK</td>
<td>--</td>
</tr>
<tr>
<td>Red Fleet</td>
<td>1.0</td>
<td>1.0</td>
<td>0.33</td>
<td>0.01</td>
<td>&lt; 0.01</td>
<td>7</td>
<td>YES*</td>
<td>Sr</td>
</tr>
<tr>
<td>McPhee</td>
<td>0.5</td>
<td>1.0</td>
<td>0.05</td>
<td>0.02</td>
<td>&lt; 0.01</td>
<td>7</td>
<td>NK</td>
<td>--</td>
</tr>
</tbody>
</table>

*Detected in larger sample size of walleye analyzed in 2011
Figure 14. Depths and elevations of reservoir outflow structures used in determining spill frequency and emigration risk.
Figure 15. Thermal optima ($T_{\text{opt}}$) of six nonnative fish species and their expected relative position in the water column during summer stratification (dashed line represents a temperature profile). Sources for $T_{\text{opt}}$ are shown for each species.
Figure 16. Aerial view of the dam on Lake Catamount in 2003 from Google Earth (North ↑).
Figure 17. Annual duration of spills at Catamount dam during 1999-2010.
Figure 18. Aerial view of the dam on Crawford Reservoir in 2012 from Google Earth (North ↑).
Figure 19. Upper panel: level of spillway (thin black line), reservoir surface (gray line), penstock (dashed line), and bottom (thick black line) at Crawford Reservoir. Mean distance between surface and penstock opening is also shown. Lower panel: annual spill duration during 1990-2010 (bars) and flow in Smith Fork Creek (line). No data (ND) were available for 1999-2004, 2008. Hydrologic year type (D = very dry, d = dry, N = normal, w = wet, W = very wet, ND = 0 = no data) is shown at top of lower panel.
Figure 20. Aerial view of the dam on Elkhead Reservoir in 2011 from Google Earth (North ↑).
Figure 21. Upper panel: level of spillway (thin black line), reservoir surface (gray line), and penstock (dashed line) at Elkhead Reservoir. Mean distance between surface and penstock opening is also shown. Lower panel: annual spill duration during the post-expansion period (2007-2012).
Figure 22. Aerial view of the dam on Flaming Gorge Reservoir in 2012 from Google Earth (North ↑).
Figure 23. Upper panel: depth of opening of selective withdrawal structures at Flaming Gorge Reservoir during 1990-2011. Lower panel: depth of opening of selective withdrawal structures (gray line), water temperature at depth of SWS opening (black line), and optimum temperature for burbot (dashed line) during 2003-2011.
Figure 24. Aerial view of the dam on Harvey Gap Reservoir in 2011 from Google Earth (North ↑).
Figure 25. Aerial view of the dam on Juniata Reservoir in 2011 from Google Earth (North ↑). Hallenbeck Reservoir is showing on the left border of the image.
Figure 26. Aerial view of the dam on Kenney Reservoir in 2011 from Google Earth (North ↑).
Figure 27. Annual spill duration at Kenney Reservoir during 2003-2006, when operations data were available.
Figure 28. Aerial view of the dam on McPhee Reservoir in 2012 from Google Earth (North ↑).
Figure 29. Level of spillway (thin black line), reservoir surface (gray line), and penstock (dashed line) at McPhee Reservoir. Mean distance between surface and penstock opening is also shown. The spillway has not been used since 1995.
Figure 30. Aerial view of the dam on Paonia Reservoir in 2012 from Google Earth (North ↑).
Figure 31. Upper panel: level of spillway (thin black line), reservoir surface (gray line), penstock (dashed line), and bottom (thick black line) at Paonia Reservoir. Mean distance between surface and penstock opening is also shown. Lower panel: annual spill duration (bars) and flow in Muddy Creek (line) during 1990-2010. Hydrologic year type (D = very dry, d = dry, N = normal, w = wet, W = very wet, 0 = no data) is shown at top of lower panel.
Figure 32. Aerial view of the dam on Red Fleet Reservoir from U.S. Bureau of Reclamation (North ↑).
Figure 33. Upper panel: level of spillway (thin black line), reservoir surface (gray line), penstock (dashed line), and bottom (thick black line) at Red Fleet Reservoir. Mean distance between surface and penstock opening is also shown. Lower panel: annual spill duration (bars) and flow in Big Brush Creek (line) during 1990-2010. Hydrologic year type (D = very dry, d = dry, N = normal, w = wet, W = very wet, ND = 0 = no data) is shown at top of lower panel.
Figure 34. Aerial view of the dam on Ridgway Reservoir in 2012 from Google Earth (North ↑).
Figure 35. Upper panel: level of spillway (thin black line), reservoir surface (gray line), penstock (dashed line), and bottom (thick black line) at Ridgway Reservoir. Mean distance between surface and penstock opening is also shown. Lower panel: annual spill duration (bars) and flow in the Uncompahgre River (line) during 1990-2010. Hydrologic year type (D = very dry, d = dry, N = normal, w = wet, W = very wet, ND = 0 = no data) is shown at top of lower panel.
Figure 36. Aerial view of the dam on Rifle Gap Reservoir in 2011 from Google Earth (North ↑).
Figure 37. Upper panel: level of spillway (thin black line), reservoir surface (gray line), penstock (dashed line), and bottom (thick black line) at Rifle Gap Reservoir. Mean distance between surface and penstock opening is also shown. Lower panel: annual spill duration (bars) and flow in Rifle Creek (line) during 1990-2010. Hydrologic year type (D = very dry, d = dry, N = normal, w = wet, W = very wet, ND = 0 = no data) is shown at top of lower panel.
Figure 38. Aerial view of the dam on Rio Blanco Reservoir in 2011 from Google Earth (North ↑).
Figure 39. Aerial view of the dam on Stagecoach Reservoir in 2011 from Google Earth (North ↑).
Figure 40. Upper panel: level of spillway (thin black line), reservoir surface (gray line), penstock (dashed line), and bottom (thick black line) at Stagecoach Reservoir. Mean distance between surface and penstock opening is also shown. Lower panel: annual spill duration during 1990-2005.
Figure 41. Aerial view of the dam on Starvation Reservoir in 2005 from Google Earth (North ↑).
Figure 42. Upper panel: level of spillway (thin black line), reservoir surface (gray line), penstock (dashed line), and bottom (thick black line) at Starvation Reservoir. Mean distance between surface and penstock opening is also shown. Lower panel: annual spill duration (bars) and flow in the Strawberry River (line) during 1990-2010. Hydrologic year type (D = very dry, d = dry, N = normal, w = wet, W = very wet, 0 = no data) is shown at top of lower panel.
PART 3. CONCLUSIONS AND RECOMMENDATIONS

Conclusions

Strontium isotope ratio ($^{87}\text{Sr}/^{86}\text{Sr}$) proved to be an excellent marker of fish provenance, with most reservoirs within a watershed possessing highly distinctive $^{87}\text{Sr}/^{86}\text{Sr}$. The $^{87}\text{Sr}/^{86}\text{Sr}$ of fish within a reservoir generally did not differ among species, and was stable through time. Known movements of tagged smallmouth bass in the Yampa River/Elkhead Reservoir system confirmed the ability of $^{87}\text{Sr}/^{86}\text{Sr}$ to trace origins and movements between reservoirs and rivers downstream. However, we also found that $^{87}\text{Sr}/^{86}\text{Sr}$ of reservoirs and their rivers downstream could be indistinguishable (e.g., McPhee/Dolores River, Kenney/White River, and Flaming Gorge/Green River). Thus, detecting downstream emigration from reservoirs using $^{87}\text{Sr}/^{86}\text{Sr}$ alone can be difficult unless fish move from a tributary to a mainstem river. In most cases we found that reservoirs on tributaries had distinct $^{87}\text{Sr}/^{86}\text{Sr}$ from the mainstem river that they flow into (e.g., Rifle Gap Reservoir/Rifle Creek/Colorado River, Elkhead Reservoir/Elkhead Creek/Yampa River).

Despite uncertainties about river and reservoir signatures, we found compelling evidence that nonnative sport fish (e.g., walleye, northern pike, smallmouth bass) have emigrated from several reservoirs into critical habitat. In cases where we had samples and water chemistry to support strong inference, we found that emigration from reservoirs had likely occurred, contributing to populations of nonnative fish in critical habitat downstream. An emigration risk index based on configuration and operations of dams differed considerably among reservoirs, but we found that emigration had likely occurred across the entire range of computed emigration risks. Thus, nearly all the reservoirs in our study pose some risk of emigration. The longer that dams lack structures limiting downstream emigration, and spill frequently, the more fish emigration to critical habitat contributes to propagule pressure and increases the likelihood that more species will become established in critical habitat below dams. Following is a summary of our assessment of fish emigration by river sub-basin.

Yampa River

Untagged smallmouth bass captured in the Yampa River in 2004 and 2008 likely did not come from Elkhead Reservoir, and within-river reproduction is possible. However, emigration of smallmouth bass from Elkhead Reservoir to the Yampa River is known to occur from recaptures of tagged fish. Northern pike captured in the Yampa River from 2004 to 2009 had $^{87}\text{Sr}/^{86}\text{Sr}$ signatures that matched Lake Catamount, but this reservoir’s $^{87}\text{Sr}/^{86}\text{Sr}$ was very similar to that of the Yampa River downstream, making definitive assessment of origins impossible from $^{87}\text{Sr}/^{86}\text{Sr}$ alone. Both Lake Catamount and Elkhead Reservoir are configured and operated in a manner conducive to fish emigration: both spill frequently and the spillways are adjacent to shore (as opposed to in the center of the dam).

Colorado River

Smallmouth bass captured in the Colorado River upstream of Grand Junction in 2005 appeared to have originated in the river, suggesting that historic emigrants established reproducing populations. However, all walleye captured in this reach of the
Colorado River in 2006 and 2007 probably escaped from Rifle Gap Reservoir. Some northern pike, first captured in this river reach in 2011, also appeared to have escaped from Rifle Gap Reservoir. This reservoir has been configured and operated in a manner that is conducive to fish emigration: its spillway is on the end of the dam, and it spills in most years. Continued sampling of otoliths from nonnative fish in the upper Colorado River could help evaluate the effectiveness of the new barrier at Rifle Gap Reservoir. Unfortunately, as with smallmouth bass, it appeared that northern pike may also be reproducing in the Colorado River based on lifetime $^{87}\text{Sr}/^{86}\text{Sr}$ profiles. Alternatively, those northern pike captured in the river with constant $^{87}\text{Sr}/^{86}\text{Sr}$ profiles could have originated from a nearby, un-fingerprinted source. Follow-up sampling and analysis are needed to evaluate origins of nonnative fish in the upper Colorado River.

**Gunnison River**

We did not have any samples of fish from below Paonia Reservoir but based on the configuration and operation of the spillway, emigration risk from Paonia Reservoir is very high. Although the reservoir was treated with piscicides in 2012, the reservoir remains a risk if nonnative fish recur. The possibility of nonnative piscivores invading the Gunnison River is alarming because this reach has been considered a de facto native fish refuge, with few nonnative piscivores present (Anderson 2005). Fish that emigrate from Paonia Reservoir downstream to the Colorado River would be indistinguishable from those arising from Rifle Gap Reservoir, based on $^{87}\text{Sr}/^{86}\text{Sr}$ signatures. Thus, the one northern pike captured below the Redlands Passage in 2011 may have originated from either Rifle Gap or Paonia Reservoir. Examination of the growth history of northern pike captured in the Colorado and lower Gunnison rivers could be useful in determining their origin. We believe that northern pike grow slowly in Paonia Reservoir and more quickly in Rifle Gap Reservoir (Johnson and Sorenson 2010).

**Green River**

Smallmouth bass captured in the Green River were classified using $^{87}\text{Sr}/^{86}\text{Sr}$ as having come from Starvation Reservoir. Thirteen walleye collected in the Green River during 2007 and 2009 also had $^{87}\text{Sr}/^{86}\text{Sr}$ signatures consistent with Starvation Reservoir. Based on a larger sample of walleye collected from the Green River (including some from 2011), we classified 41 of the fish to Starvation Reservoir and two to Red Fleet Reservoir. The remaining nine fish had $^{87}\text{Sr}/^{86}\text{Sr}$ that suggested they originated in the Green River itself. Origins of northern pike captured in the Green River were difficult to determine but some $^{87}\text{Sr}/^{86}\text{Sr}$ were consistent with fish from the Yampa River. There remains uncertainty about the true origins of nonnative fish captured in the Green River. We suspect that the Duchesne River may have the same $^{87}\text{Sr}/^{86}\text{Sr}$ as Starvation Reservoir. Thus, nonnative fish moving from that system into the Green River could be naturally reproducing in the Duchesne River instead of emigrating from Starvation Reservoir. This could be evaluated with sampling for juvenile fish in the river. We also found that the $^{87}\text{Sr}/^{86}\text{Sr}$ of Lake Powell was similar to that of Starvation Reservoir, so it is possible that some of the fish captured in the Green River moved upstream from Lake Powell. This seems unlikely given the distance involved and the fact that no fish captured in the Upper Colorado River had $^{87}\text{Sr}/^{86}\text{Sr}$ consistent with Lake
Powell. Investigating additional geochemical markers could help resolve this uncertainty.

**Recommendations**

- In cases where reservoir and river $^{87}$Sr/$^{86}$Sr are similar intensive sampling in rivers downstream from dams could evaluate the likelihood that nonnative fish are reproducing in the river vs. arising from reservoir emigration. The absence of juvenile fish in such samples would support reservoir origins.

- Comparison of growth histories of reservoir fish and river-resident fishes should also be used to infer the origin of river-caught fish, especially in locations where the growth rates are expected to differ between the two environments. For instance, if reservoir fish grow quickly early in life and slower in the river downstream, then back-calculation could be used to determine earlier size at age and the likely rearing environment.

- More research is needed to find additional natural markers that can supplement $^{87}$Sr/$^{86}$Sr for distinguishing river-resident fish from fish that may have escaped from a reservoir upstream.

- If such markers can be identified, then studies should be conducted to a) evaluate the effectiveness (and cost-benefit) of fish screens on dam outflows, and b) evaluate the degree of natural reproduction of nonnative fish occurring in rivers.

- If it can be shown that the majority of a nonnative species captured in rivers originated from a reservoir then suppression of these riverine fish may be feasible once further reservoir emigration is prevented. The prospects for successfully suppressing walleye and northern pike in the Green and Colorado rivers should be investigated.

- No samples of fish from below Kenney, Paonia, Crawford, Ridgway, and Stagecoach reservoirs were available. To these fill gaps, sampling nonnative fish from the White River (below Kenney Reservoir), the North Fork of Gunnison River (below Paonia Reservoir), the Gunnison River (upstream from confluence with Colorado River to Delta), Smith Fork Creek (below Crawford Reservoir), the Uncompahgre River (downstream of Ridgway Reservoir), and the Yampa River (below Stagecoach Reservoir and above Lake Catamount) should be conducted.

- Until more is known about factors driving nonnative fish movement past dams, emigration barriers and altered dam operations that 1) minimize spills and 2) keep the reservoir surface as far above penstocks as practical may be effective approaches to minimizing downstream emigration of nonnative sport fish. Because of the diversity of reservoirs in the Basin, Recovery Program partners and dam managers should collaborate on a case-by-case basis to explore water management schemes that could achieve operational objectives.
while minimizing operations that could exacerbate emigration of nonnative fish from reservoirs into critical habitat.

- Given the prevalence of fish emigration from reservoirs, stocking of new nonnative species, by agencies and the public, should be discouraged
APPENDIX: Project publications and presentations


