Using nitrogen stable isotopes to detect long-distance movement in a threatened cutthroat trout (*Oncorhynchus clarkii utah*)

Adam J. Sepulveda, Warren T. Colyer, Winsor H. Lowe, and Mark R. Vinson

Abstract: Interior cutthroat trout occupy small fractions of their historic ranges and existing populations often are relegated to headwater habitats. Conservation requires balancing protection for isolated genetically pure populations with restoration of migratory life histories by reconnecting corridors between headwater and mainstem habitats. Identification of alternative life history strategies within a population is critical to these efforts. We tested the application of nitrogen stable isotopes to discern fluvial from resident Bonneville cutthroat trout (BCT; *Oncorhynchus clarkii utah*) in a headwater stream. Fluvial BCT migrate from headwater streams with good water quality to mainstem habitats with impaired water quality. Resident BCT remain in headwater streams. We tested two predictions: (*i*) fluvial BCT have a higher $\delta^{15}N$ than residents, and (*ii*) fluvial BCT $\delta^{15}N$ reflects diet and $\delta^{15}N$ enrichment characteristics of mainstem habitats. We found that fluvial $\delta^{15}N$ was greater than resident $\delta^{15}N$ and that $\delta^{15}N$ was a better predictor of life history than fish size. Our data also showed that fluvial and resident BCT had high diet overlap in headwater sites and that $\delta^{15}N$ of lower trophic levels was greater in mainstem sites than in headwater sites. We conclude that the high $\delta^{15}N$ values of fluvial BCT were acquired in mainstem sites.

Résumé : Les truites fardées de l'intérieur du continent n'occupent plus que de petites portions de leur aire de répartition du passé et les populations actuelles sont souvent confinées aux habitats d'amont. Leur conservation nécessite un équilibre entre la protection des populations isolées génétiquement pures et le rétablissement du cycle biologique migrateur en restituant les corridors qui relient les habitats d'amont et ceux du cours principal. Il essentiel dans ces efforts d'identifier les stratégies de rechange des cycles biologiques au sein des populations. Nous avons testé l'utilisation des isotopes stables d'azote pour reconnaître les formes fluviales et résidentes de la truite fardée de Bonneville (BCT; *Oncorhynchus clarkii utah*) dans un cours d'eau d'amont. Les BCT fluviales migrent des cours d'eau d'amont à qualité d'eau supérieure vers les habitats du cours principal qui ont une qualité d'eau dégradée. Les BCT résidentes demeurent dans les cours d'eau d'amont. Nous avons vérifié deux prédictions: (*i*) les BCT fluviales ont une valeur de $\delta^{15}N$ plus élevée que celle des résidentes et (*ii*) les valeurs de $\delta^{15}N$ des BCT fluviales reflètent leur alimentation et l'enrichissement en $\delta^{15}N$ caractéristique des habitats du cours principal. Nous observons que le $\delta^{15}N$ des truites fluviales est plus élevé que le $\delta^{15}N$ des résidentes et que $\delta^{15}N$ est une meilleure variable explicative du cycle biologique que ne l'est la taille du poisson. Nos données montrent aussi que les BCT fluviales et résidentes ont un fort chevauchement de régime alimentaire dans les sites d'amont et que les valeurs de $\delta^{15}N$ des niveaux trophiques inférieurs sont plus élevées dans les sites du cours principal que dans les sites d'amont. Nous en concluons que les valeurs élevées de $\delta^{15}N$ des BCT fluviales ont été acquises dans les sites du cours principal.

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Introduction

Long-distance movements (LDMs) of individuals influence fundamental ecological and evolutionary processes, including population persistence and gene flow (e.g., Gross 1987; Lowe et al. 2006). However, the frequency and scale of LDMs are difficult to quantify because these events may be rare (Kareiva 1983; Nathan 2001; Lowe 2003) and often require extensive sampling to detect (Koenig et al. 1996; Skalski and Gilliam 2000). Recent studies using radiotelemetry, mark–recapture tagging, and genetic markers indicate that stream resident fish move more than previously thought (Gowan and Fausch 1996; Colyer et al. 2005; Wofford et al. 2005), but quantifying the frequency of fish LDMs, which include migration and dispersal, remains difficult because of methodological constraints (reviewed in Bohonak 1999; Roussel et al. 2000; Albanese et al. 2003).

Long-distance movements in native trout populations often are indicative of migratory life history strategies once

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A.J. Sepulveda[1] and W.H. Lowe. Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA.
W.T. Colyer. Trout Unlimited, 249 South 100th West, Providence, UT 84332, USA.
M.R. Vinson. US Geological Survey, Great Lakes Science Center, Lake Superior Biological Station, 2800 Lake Shore Drive, Ashland, WI 54806, USA.

[1]Corresponding author (e-mail: adam.sepulveda@mso.umt.edu).

common, but now rare, across most interior cutthroat subspecies. Anthropogenic activities during the past century have fragmented habitats and imposed selective pressures against migrations, causing declines in fluvial populations and, ultimately, the extirpation of cutthroat populations from many large river habitats (Young 1995). Most genetically pure cutthroat trout populations now comprise resident individuals isolated in higher-elevation tributary systems. Conservation of native trout populations has become a balancing act between maintaining genetic purity by isolating populations from nonnative invaders and protecting life history diversity by restoring migration corridors and reconnecting fragmented habitats. This trade-off is the subject of recent research, and models hinge, to some extent, on accurately identifying alternative life histories and characterizing migratory behaviors within a given population (Fausch et al. 2006; Peterson et al. 2008). In this study, we investigated the use of nitrogen stable isotopes in identifying migratory strategies within a population.

Nitrogen stable isotopes are commonly used to identify trophic interactions within a food web (e.g., Vander Zanden et al. 1997) and as water pollution indicators (e.g., Harrington et al. 1998). The ratio of ^{15}N to ^{14}N ($\delta^{15}N$) provides information about an individual's diet because it is typically enriched 3‰–4‰ from prey to predator (Cabana and Rasmussen 1996). Within the same food web, insectivorous fish are predicted to have lower $\delta^{15}N$ than piscivorous fish. The $\delta^{15}N$ of stream organisms also changes across space due to human land use. The influx of ^{15}N-enriched nitrate from certain fertilizers, soil organic matter, and sewage raises $\delta^{15}N$ levels in aquatic food webs within agricultural or urban catchments relative to upstream catchments that are minimally disturbed (Heaton 1986; Harrington et al. 1998).

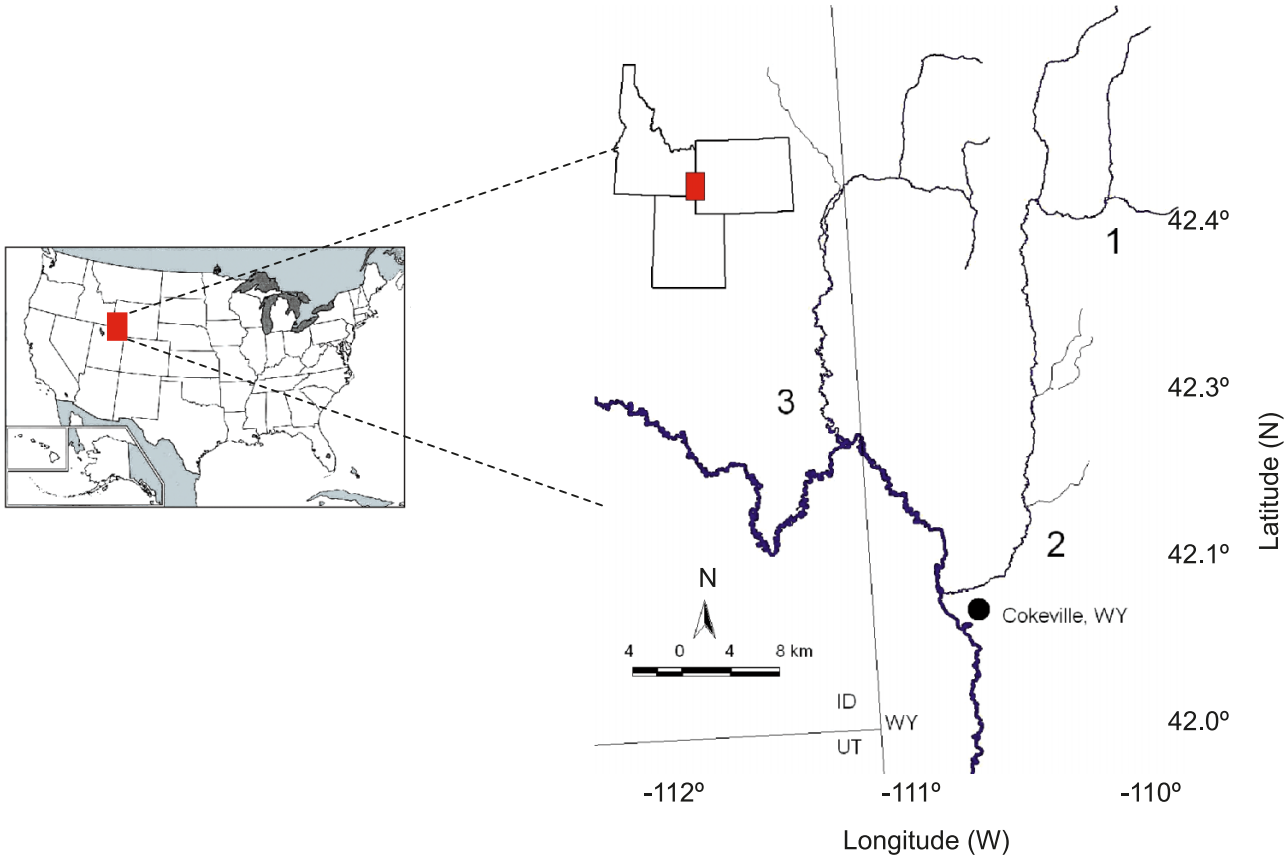
We hypothesize that spatial differences in $\delta^{15}N$ due to catchment land use can be used to identify individuals that move between human-disturbed and minimally disturbed stream habitats. This technique has been used to assess marine fish movement in coastal areas exposed to $\delta^{15}N$-rich sewage (Hansson et al. 1997) but has not been applied in streams, despite the common pattern of reduced water quality and increased human contaminants along the longitudinal stream continuum. The use of $\delta^{15}N$ to study LDM in streams has been minimal because downstream flow and variable diets often make site-specific signatures indistinct (but see Gray et al. 2004; Kennedy et al. 2005). The novel contribution of our work is the use of natural versus anthropogenic variation of N stable isotopes that occurs along the stream network to identify LDM in a threatened fish nonlethally.

In this study, we test the use of $\delta^{15}N$ as an identifier of LDM in Bonneville cutthroat trout (BCT; *Oncorhynchus clarkii utah*), a stream fish that exhibits both fluvial and resident life history strategies in the Bear River system of Wyoming, Idaho, and Utah (Fig. 1) (Schrank and Rahel 2004; Colyer et al. 2005). Fluvial individuals use lower-elevation mainstem rivers for growth and migrate up to 90 km to headwater habitats to spawn (Colyer et al. 2005). Resident forms complete their entire life cycle within a limited portion of a single stream. Fluvial fish grow larger than most residents because of a putative diet shift to piscivory in mainstem rivers (Schrank and Rahel 2004; Colyer et al. 2005). Because fecundity increases with body size (Wooton 1979), fluvial fish can have large effects on population dynamics (Dunham et al. 2002; Fausch et al. 2006). However, the fluvial life history strategy is threatened because irrigation diversion structures reduce or eliminate access to upstream spawning habitats and entrain downstream migrants in irrigation canals that are dewatered (Schrank and Rahel 2004; Colyer et al. 2005). The Bear River watershed is one of few remaining BCT strongholds and harbors one of the last remaining cutthroat populations with a fluvial component. BCT are designated as "sensitive" by the USDA Forest Service and Wyoming, are a "species of concern" in Utah and Idaho, and have been petitioned for federal listing. As a result, it is urgent to understand the frequency of BCT fluvial movements and the importance of stream connectivity.

The number of fluvial fish that return to headwater habitats is unknown, though parasite load and size help discriminate returning fluvial fish from resident fish and those that have not yet made fluvial, downstream movements (hereafter also referred to as resident fish). Many fluvial fish captured in headwater tributaries have sand-grain-sized black spots on their skin that result from *Apophallus imperator*, a trematode parasite acquired in the mainstem Bear River (D. Teuscher, Senior Fisher Research Biologist, Idaho Department of Fish and Game, Boise, Idaho, personal communication). However, not all fluvial fish show visible signs of *A. imperator*, and the infection rate and frequency are unknown. Fish size also fails to separate fish that recently made fluvial movements from those that have made fluvial movements in previous years but currently remain resident in headwater tributaries. Because parasite load and size can be ambiguous, there is a need for an accurate and reliable marker of fluvial fish.

We capitalized on upstream–downstream differences in BCT diet, catchment land use, and parasite load (i.e., *A. imperator*) to test the use of $\delta^{15}N$ as a marker of fluvial BCT movements in the Bear River watershed. Fluvial BCT that move to lower-elevation stream reaches are known to have increased rates of piscivory relative to resident fish (Nielson and Lentsch 1988; Colyer et al. 2005). In addition, these lower-elevation stream reaches are surrounded by agricultural lands and have nitrate concentrations that exceed EPA water quality standards (Wyoming Department of Environmental Quality (Wyoming DEQ) 2004). In contrast, headwater tributaries are minimally disturbed and meet EPA water quality standards (Wyoming DEQ 2004). We predicted that fluvial BCT (i.e., those with *A. imperator*) in the Bear River watershed would have higher $\delta^{15}N$ values than resident fish in headwater tributaries. To test this prediction, we compared $\delta^{15}N$ values in fluvial BCT with values in resident BCT and resident brown trout (BNT; *Salmo trutta*) sampled in headwater tributaries in 2005 and 2006. To test our two main predictions that higher fluvial BCT $\delta^{15}N$ values reflect (*i*) downstream diet differences and (*ii*) downstream $\delta^{15}N$ enrichment, we sampled BCT and BNT stomach contents and the $\delta^{15}N$ of multiple trophic levels at both mainstem and headwater sites in the Bear River watershed.

Fig. 1. Map of the Bear River watershed with Smiths Fork and Thomas Fork drainages (ID, Idaho; WY, Wyoming; UT, Utah; inset shows location in USA). Study sites were located at (1) Hobble Creek, (2) the lower Smiths Fork, and (3) near the confluence of Thomas Fork and Bear River.



Materials and methods

Study site

This study was conducted in 2005 and 2006 at two drainages in the Bear River watershed, Lincoln County, Wyoming, USA (Fig. 1): (*i*) within the Smiths Fork drainage (427 km^2), and (*ii*) at the confluence of the Thomas Fork drainage (293 km^2) with the mainstem of Bear River. Headwater reaches of Smiths Fork, including Hobble Creek (third-order stream with a drainage area of 111 km^2), are relatively pristine, heavily forested, and have good water quality (Wyoming DEQ 2004). Lower portions of Smiths Fork, Thomas Fork, and the mainstem of Bear River are listed as water quality impaired because of excess suspended sediments, fecal coliform, and high levels of nutrients, including nitrogen and nitrate (Wyoming DEQ 2004). Primary land uses are cattle rangeland (73%) and hay agriculture (10%).

Fish community composition changes along the Bear River watershed. In Hobble Creek, BCT occur with BNT, mountain whitefish (*Prosopium williamsoni*), sculpin (*Cottus bairdi* and *Cottus beldingi*), and mountain sucker (*Catostomus platyrhynchus*). A different community composition occurs downstream in Smiths Fork, Thomas Fork, and Bear River, including species such as Utah sucker (*Catostomus ardens*), longnose dace (*Rhinichthys cataractae*), and common carp (*Cyprinus carpio*).

Fluvial and resident fish identification

During 2005 and 2006, there was widespread occurrence of the parasite *A. imperator* in lower-elevation habitats of the Bear River watershed (D. Teuscher, Idaho Department of Fish and Game, Boise, Idaho, personal communication). Infection produces visible, black cysts in fish dermal tissue. We believe that *A. imperator* is an excellent indicator for fluvial fish that spend time in the mainstem Bear River as *A. imperator* is associated with large, mainstem agricultural rivers rather than tributaries (Steedman 1991).

During our study, we never observed *A. imperator* in resident fishes in Hobble Creek or in the upper reaches of Thomas Fork Creek. In four years of trapping in these tributaries, we only observed the parasite in large BCT (>325 mm total length, TL) that were likely fluvial. To test our hypothesis, we operated a bypass fish trap at a river-wide irrigation diversion in lower Thomas Fork Creek and a two-way picket weir in upper Thomas Fork Creek from June through September 2006. Our lower trap was located 2 km upstream from the confluence with Bear River, and our upper trap was located 35 km upstream in Thomas Fork. We recorded the occurrence of *A. imperator* on all fish species captured. We only report results from fish species that were captured in both the lower and upper traps. In addition, we recorded the occurrence of *A. imperator* on all BCT and BNT sampled in a two-way picket weir operated in Hobble Creek from June through October in 2005 and 2006. All

traps were checked twice daily and sampled fish were finclipped to avoid resampling.

In our analyses of $\delta^{15}N$, we compared four fish groups: fluvial BCT, resident BCT, unknown BCT, and large BNT. Fluvial BCT were those with visible signs of *A. imperator*. We declared resident BCT as those measuring <200 mm TL, because they had foraged only in Hobble Creek. Our trap captures indicate that these fish had not yet made fluvial movements. Unknown BCT were 200–600 mm TL and had no visible sign of *A. imperator*. To test the assumption that fluvial life history rather than fish size influences $\delta^{15}N$ values, we compared $\delta^{15}N$ values of fluvial BCT with those of large BNT, which were >350 mm TL. BNT $\delta^{15}N$ values provided a reference point for comparison because data from a two-way picket weir operated in 2003–2006 suggested that BNT are resident to Hobble Creek and did not move to downstream reaches. We did not test for brown trout movement in the winter; however, multiple studies on stream brown trout in their nonnative range suggest that winter movement is restricted (Meyers et al. 1992; Brown et al. 2001; but see Burrell et al. 2000).

Fluvial and resident $\delta^{15}N$ comparison

To determine if fluvial BCT had distinct $\delta^{15}N$ values, we sampled BCT and BNT captured in Hobble Creek in the summers of 2005 and 2006. We constructed a two-way picket weir in Hobble Creek to capture all BCT and BNT greater than 100 mm TL moving upstream and downstream. We also captured fish above the weir using a backpack electroshocker and by angling in pool, riffle, and run mesohabitats. We recorded length of all captured fish. The variety of capture methods ensured that samples were representative of BCT and BNT populations and not of a subset of related individuals with high activity rates or similar foraging behavior.

In 2005, we collected samples during two 7-day periods: 14–20 June (early summer) and 29 July – 4 August (midsummer). In 2006, we only sampled in the early summer. Fish tissue samples were collected from below the dorsal fin with a 3 mm diameter dermal biopsy punch (Miltex Instrument Company, Bethpage, New York). Samples were stored on ice and then frozen until processed (Bosley and Wainright 1999). Samples were dried for 48 h at 65 °C (Midwood and Boutton 1998), ground to a fine powder, and packed in 4 × 6 mm tin capsules. $\delta^{15}N$ was measured using a Europa Hydra 20/20 continuous-flow isotope-ratio mass spectrometer (PDZ Europa Ltd., Cheshire, UK) at the University of California–Davis Stable Isotope Facility (Davis, California, USA). Stable isotope content is reported as $\delta^{15}N$ (units of ‰) and defined as

$$\delta^{15}N = \left[\left(\frac{R_{SAMPLE}}{R_{STANDARD}}\right) - 1\right] \times 1000$$

where R_{sample} is the $\delta^{15}N$ of the sample and $R_{standard}$ is the $\delta^{15}N$ of the reference standard, atmospheric nitrogen. Average analytical error, estimated as the standard deviation of the isotopic ratio of an internal standard, was 0.17‰ (n = 34). Precision for internal reference material run concurrently with our samples was ±0.3‰.

To test the use of $\delta^{15}N$ as a fluvial marker, we compared $\delta^{15}N$ values among three fish groups: fluvial BCT with *A. imperator*, resident BCT 100–200 mm TL, and large BNT >350 mm TL. We used analysis of covariance (ANCOVA) to assess variation in $\delta^{15}N$ between our three fish groups. Fish group, season (early summer 2005, midsummer 2005, and early summer 2006), and fish group × season were initially entered as sources of variability. Fish total length was entered as a continuous covariate.

We used normal mixture clustering analysis (NMCA; JMP 7, SAS Institute Inc., Cary, North Carolina) as an a posteriori tool to assess the accuracy of fluvial and resident classifications and to test the assignment of BCT with unknown life histories. NMCA estimates the probability that a data point is assigned to a cluster through an iterative process and is appropriate where clusters have points that overlap (McLachlan and Krishnan 1997). To test the robustness of NMCA, we used two seeding methods to define our clusters. First, we used NMCA to organize the $\delta^{15}N$ values of only known fluvial and known resident individuals in 2005 and 2006 into two clusters. Cluster center 1 was the mean of all fluvial BCT $\delta^{15}N$ values and cluster center 2 was the mean of all resident BCT $\delta^{15}N$ values. Unknown BCT were than assigned probability-based membership to the fluvial or resident cluster. Second, we used NMCA to organize the $\delta^{15}N$ values of all BCT sampled (fluvial, resident, and unknown) in 2005 and 2006 into two clusters. All BCT were then assigned probability-based membership to one of two clusters. Assignment probabilities of unknown BCT were identical for both cluster-seeding methods, so we only report results for the second seeding method because it requires no a priori assumptions.

To test the accuracy of using only $\delta^{15}N$ to discern between fluvial and resident individuals, we compared the number of known fluvial BCT (based on presence of *A. imperator*) and known resident BCT (based on size) assigned to the cluster with the higher mean $\delta^{15}N$ and the cluster with the lower mean $\delta^{15}N$, respectively, using seed method 2. Finally, we investigated the use of BCT total length to discern fluvial from resident individuals by determining to which cluster (low or high $\delta^{15}N$) unknown BCT were assigned using seeding method 1. We divided unknown BCT into two size-based groups, <350 mm TL and >350 mm TL, based on the observations that all known fluvial individuals were >350 mm TL and that 350 mm could be a key size threshold for predicting life history.

Diet analysis

We sampled BCT and BNT stomach contents in early and mid-summer in 2005 to test the following prediction: higher $\delta^{15}N$ values in fluvial BCT result from foraging in lower-elevation, downstream reaches and not differences in what fluvials and residents are eating in headwater reaches. We compared the occurrence and abundance of invertebrates and fish in the diets of fluvial BCT, resident BCT, and large BNT sampled in Hobble Creek. We used gastric lavage (Elliot 1972) to collect stomach contents from the same fish that were used for $\delta^{15}N$ analysis. However, we did not sample stomach contents from fish captured in the picket weir because feeding behavior may have been altered while they were in the trap boxes.

We classified stomach contents into the following prey

categories: Annelida, Coleoptera, Diptera, Ephemeroptera, fish, Hemiptera, Plecoptera, terrestrial insects, Trichoptera, and vegetation–detritus. We divided the wet weight (grams) of stomach contents by wet weight (grams) of the fish and multiplied by 100 to yield a relative stomach content weight (RW) for each fish. Fish with a RW <0.1% were considered to have empty stomachs and were excluded from our final data set (Angradi and Griffith 1990). Fish with >25% (by mass) of unidentifiable contents were also excluded (McHugh et al. 2007).

We described diet composition using the percent dietary overlap index of Schoener (1970):

$$\text{Percent overlap} = \left[1 - 0.5\left(\sum_{i=1}^{n} |P_{ij} - P_{ik}|\right)\right] \times 100$$

where P_{ij} and P_{ik} are the mean percent abundance of prey item i in the stomach of group types j and k, respectively. This index expresses diet similarity between two groups on a scale from 0% to 100%, with 100% indicating complete dietary overlap. Biologically meaningful diet overlap is indicated by values exceeding 60% (Schoener 1970). We conducted the following comparisons of percent dietary overlap: fluvial BCT vs resident BCT, fluvial BCT vs large BNT.

Piscivory can increase δ^{15}N values, so we calculated occurrence and importance of fish prey in the sampled stomach contents. To compare the importance of fish prey in diets, we computed the index of relative importance (%IRI) (Cortés 1997; McHugh et al. 2007). This is a composite measure of the percent occurrence ($\%O_i$), percent abundance by number ($\%N_i$), and gravimetric importance by weight ($\%W_i$) of all fish stomachs containing any individuals of a given prey category, i. Prey categories were identical to those used for computing the Schoener dietary index. We computed %IRI as

$$\text{IRI}_i = [\%O_i \cdot (\%N_i + \%W_i)]$$

$$\%\text{IRI}_i = \left[\text{IRI}/\left(\sum \%\text{IRI}_i\right)\right] \times 100$$

To assess the role of piscivory, we used Wilcoxon ranked-sum tests to compare the effect of season on $\%N$ and %IRI within five fish groups: fluvial BCT, resident BCT, large BNT, BCT 200–350 mm TL, and BNT <350 mm TL. If there were no seasonal differences, samples were pooled within each group. We then used Mann–Whitney – Wilcoxon ranked-sum tests to compare $\%N$ and %IRI of fish among the five fish groups.

Trophic-level comparison

To test our prediction that mainstem habitat sites with poor water quality have higher δ^{15}N values than headwater reaches with good water quality, we sampled δ^{15}N values of primary and secondary trophic levels (i.e., periphyton, stream invertebrates, and prey fish) in Hobble Creek and in the two mainstem habitat sites (lower Smiths Fork and Thomas Fork of Bear River (Fig. 1)) in July of 2006. In Hobble Creek, we collected periphyton and stream invertebrates 200 m upstream from the picket weir. We sampled prey fish from the picket weir's trap boxes. In lower Smiths Fork, periphyton and invertebrates were collected 20 km upstream of Cokeville, Wyoming (Fig. 1), but we were not permitted to capture prey fish at this site. In Thomas Fork, we collected periphyton, invertebrates, and prey fish at the Peterson Diversion (Bear Lake County, Idaho), which is <2 km upstream of the confluence with the Bear River mainstem and has similar water quality and biotic composition to the mainstem (Wyoming DEQ 2004). Colyer et al. (2005) tracked large BCT from Hobble Creek to the Peterson Diversion of Thomas Fork using radiotelemetry; therefore, we are confident that these locations are representative of habitat that fluvial fish use for foraging. Because of its proximity to Bear River, we refer to the Thomas Fork sample site as Bear River in analyses.

Periphyton samples were collected from three random 1 m^2 plots within a 10 m reach at each location in July of 2006. We scraped the biofilm off three to five rocks per plot (Zah et al. 2001) and removed all macroinvertebrates found. Within the same 10 m reach, we took six random Surber samples of stream invertebrates by disturbing rocks for 30 s within a 0.093 m^2 quadrant. Stream invertebrates were sorted to order. We used the same protocol to sample δ^{15}N from prey fish as we did for BCT and BNT. All samples of periphyton, stream invertebrates, and prey fish tissue were immediately put on ice and frozen until processed. We used the same methods to prepare these trophic level samples for δ^{15}N analysis as were used for BCT and BNT fish tissue; however, invertebrate samples consisted of one to seven individuals from the same order and reach to ensure enough dry mass for isotopic analysis.

To assess spatial variation of δ^{15}N between upstream and downstream sites, we compared δ^{15}N values of each trophic level among the three locations. We pooled all stream invertebrates and prey fish δ^{15}N values at each location into two coarse trophic levels: stream invertebrates and prey fish. Invertebrate and prey fish species known to be sensitive to poor water quality, such as Plecoptera and sculpin, were absent in lower Smiths Fork and Bear River. Because our main concerns were the effect of location on δ^{15}N values and the relative difference between trophic levels, and because we were not attempting to identify the specific diet composition of fish using stable isotopes, we believe that a coarse-level analysis is sufficient. We used analysis of variance (ANOVA) to test the effect of location on the δ^{15}N values of stream invertebrates and prey fish. For periphyton δ^{15}N values, we used Kruskal–Wallis tests to assess the effect of location because values were not normally distributed. All statistical analyses were done in JMP (version 7, SAS Institute Inc., Cary, North Carolina).

Results

A. imperator occurrence

We documented *A. imperator* extensively in small resident prey fish species at our lower-elevation trap in Thomas Fork and rarely at our upstream trap (Table 1). At the lower trap, we documented *A. imperator* in 57% of all sampled resident fishes, but we documented only one case of *A. imperator* in resident fishes in the upper traps. In Hobble Creek, *A. imperator* was never detected in resident BCT (n = 400) and BNT (n = 162); however, it was detected in 36% of BCT >348 mm TL) (n = 280) in 2005 and 2006.

Table 1. Percent occurrence of *A. imperator* in fish species (percent infected) and abundance of fish species (*n*) found in both the lower trap, near the confluence of Thomas Fork Creek with Bear River, and the upper trap, 35 km upstream from the confluence.

	Lower trap		Upper trap	
Species	% infected	*n*	% infected	*n*
Utah sucker (*Catostomus ardens*)	3.7	190	0.0	17
Longnose dace (*Rhinichthys cataractae*)	10.6	47	1.9	51
Speckled dace (*Rhinichthys osculus*)	59.0	6 841	0.0	10
Redside shiner (*Richardsonius balteatus*)	56.0	5 129	0.0	10
Total	56.7	12 207	1.1	88

Table 2. Total length (mm) and $\delta^{15}N$ values of known fluvial and known resident Bonneville cutthroat trout (BCT; *Oncorhynchus clarkii utah*) and brown trout (BNT; *Salmo trutta*) sampled in early summer (12–20 June) and midsummer (1–8 August) in Hobble Creek, Wyoming, during 2005 and 2006.

				Total length (mm)			$\delta^{15}N$	
Season	Species	Group	*N*	Mean	SE	Range	LS Mean	95% CI
2005, early summer	BCT	Fluvial	8	412	9.59	358–476	13.14	12.38–13.90
2005, midsummer	BCT	Fluvial	10	413	9.66	373–456	11.92	11.14–12.70
2006, early summer	BCT	Fluvial	11	446	15.68	390–570	11.47	10.43–12.51
2005, early summer	BCT	Resident	8	150	6.22	117–190	10.24	9.26–11.22
2005, midsummer	BCT	Resident	11	150	7.37	125–184	10.08	9.08–11.08
2006, early summer	BCT	Resident	6	140	7.12	117–167	9.17	8.07–10.27
2005, early summer	BNT	Resident	6	400	14.40	354–428	9.53	8.71–10.35
2005, midsummer	BNT	Resident	3	372	6.51	365–385	9.33	8.49–10.17

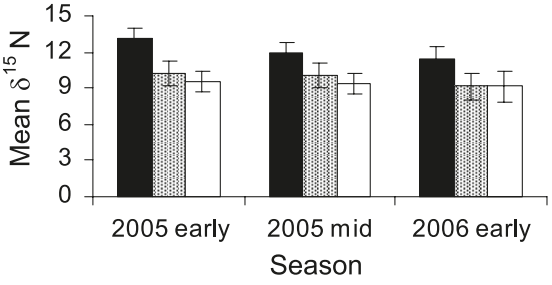
Note: The mean, standard error (SE), and range of total length are based on observed values. Least square (LS) means of $\delta^{15}N$ and the 95% confidence intervals (CI) have total length as a covariate and season, species, and group as sources of variability.

Fluvial and resident $\delta^{15}N$ comparisons

We analyzed samples from 35 BCT and 10 BNT in 2005 and 12 BCT in 2006 (Table 2). Fluvial BCT were always larger than resident BCT, but fluvial BCT and large BNT had similar lengths (Table 2). The $\delta^{15}N$ least square mean values significantly varied between fish groups (Table 2; Fig. 2) ($F_{[2,56]} = 41.55$, $P < 0.0001$; Tukey's honestly significant difference (HSD): fluvial BCT > resident BCT = large BNT). The magnitude of these $\delta^{15}N$ differences varied between seasons ($F_{[2,56]} = 7.77$, $P < 0.0012$; Tukey's HSD: early summer 2005 > midsummer 2005 = early summer 2006), but there was no interaction between fish group and season ($F_{[4,56]} = 2.04$, $P = 0.10$). In the early summer, fluvial BCT $\delta^{15}N$ was 4.7‰ greater than resident BCT and 3.8‰ greater than BNT. In midsummer, fluvial BCT $\delta^{15}N$ was 3.8‰ greater than resident BCT and 3.3‰ greater than BNT. In 2006, fluvial BCT $\delta^{15}N$ was 4.5‰ greater than resident BCT.

Cluster analyses indicated that $\delta^{15}N$ is a better tool for discrimination than fish size alone for individuals >350 mm TL (Fig. 3). For the second seeding method, the mean of the lower cluster was 9.79‰ ± 1.62‰ (standard deviation, SD) and the mean of the higher cluster was 13.28‰ ± 0.74‰ (SD). All known resident BCT ($n = 26$) were assigned to the cluster with the lower mean $\delta^{15}N$, and 18 fluvial BCT ($n = 22$) were assigned to the cluster with the higher mean $\delta^{15}N$. We sampled 61 unknown BCT, 45 of which were assigned to the lower cluster and 16 were assigned to the higher cluster. Thirty-one of 32 unknown BCT < 350 mm TL were assigned to the lower cluster, which described the $\delta^{15}N$ of known resident BCT. However, size was a poor predictor of life history for unknown individuals >350 mm TL. Fourteen individuals were assigned to the lower cluster and 15 were assigned to the higher cluster, which described the $\delta^{15}N$ of known fluvial BCT. Resident assignments occurred in unknown BCT that were 336–570 mm TL.

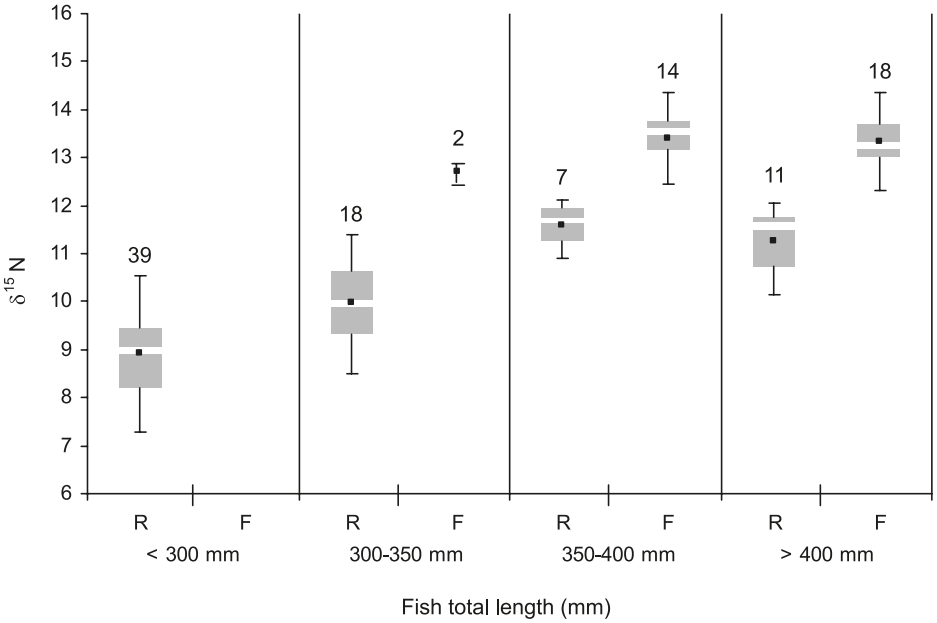
Fig. 2. Least square means of $\delta^{15}N$ for fluvial Bonneville cutthroat trout (BCT (*Oncorhynchus clarkii utah*); solid bars), resident (BCT; stippled bars), and large brown trout (BNT (*Salmo trutta*); open bars) in early summer 2005, midsummer 2005, and early summer 2006. Least square means of $\delta^{15}N$ are corrected for fish total length (mm). Vertical lines for each value are 95% confidence intervals.



Diet analysis

In 2005, we sampled 67 BCT and 50 BNT stomachs. We excluded 12 stomachs (BCT, $n = 9$; BNT, $n = 3$) from analyses because they were empty or contained a majority of unidentifiable material. Stomach analyses were based on 58 BCT and 47 BNT. Of these fish, 14 BCT were assumed to be fluvial because they had visible signs of *A. imperator*. There were few seasonal differences in the composition

Fig. 3. Box-and-whisker plots of the $\delta^{15}N$ values of individuals with known and unknown life histories in total length (mm) bins assigned to the resident cluster (R) or the fluvial cluster (F) using normal mixture cluster analysis (seeding method 2). The bottom of the box is the 25th percentile and the top is the 75th. The whiskers extend to the highest and lowest $\delta^{15}N$ values. The mean (■) and median $\delta^{15}N$ are plotted within each box. Sample size is shown above the upper whisker.



(*%N*) and relative importance (%IRI) of each prey category within each fish group, so we pooled early summer and midsummer samples.

Schoener diet overlap calculations indicate that fluvial BCT and resident BCT had a 78% diet overlap and fluvial BCT and BNT had a 75% diet overlap. Fluvial BCT and large BNT both exhibited piscivory (Table 3). However, four large BNT stomachs ($n = 10$) had evidence of piscivory and only two fluvial BCT stomachs ($n = 14$) had evidence of piscivory. Large BNT had greater *%N* ($U = 203$, $Z = 2.27$, $P = 0.02$) and %IRI ($U = 205$, $Z = 1.98$, $P = 0.02$) for the fish prey category. This trend was also supported by stomach content analyses of smaller (<350 mm TL) BCT and BNT. We did not find fish in stomachs of any BCT <350 mm TL ($n = 18$), but stomachs of two BNT <350 mm TL ($n = 21$) contained fish.

Trophic-level comparisons

Periphyton

We analyzed $\delta^{15}N$ values from three composite periphyton samples from each study location (Fig. 4). There was an effect of location on $\delta^{15}N$ values (ANOVA: $F_{[2,6]} = 87.49$, $P < 0.001$; Tukey HSD: Bear River > Smiths Fork > Hobble Creek). Values in Bear River were 3.1‰–7.5‰ greater than values in Hobble Creek.

Stream invertebrates

We analyzed $\delta^{15}N$ values from 10 samples at Hobble Creek and six samples at each downstream study location. Samples contained individuals from the following orders: Diptera, Ephemeroptera, Plecoptera, and Trichoptera. There was a significant difference in macroinvertebrate $\delta^{15}N$ values (ANOVA: $F_{[2,13]} = 5.95$, $P = 0.01$; Tukey HSD: Bear River = Smiths Fork > Hobble Creek).

Table 3. Percent occurrence of piscivory within Bonneville cutthroat trout (BCT; *Oncorhynchus clarkii utah*) and brown trout (BNT; *Salmo trutta*) total length (TL) size classes (mm).

Size class (mm TL)	*N* (BCT, BNT)	% Piscivory (BCT, BNT)
100–200	5, 8	0, 0
200–300	5, 8	0, 25
300–350	8, 5	0, 0
>350	14, 10	13, 40
Total	32, 31	6, 17

Note: Early summer and midsummer stomach samples were pooled.

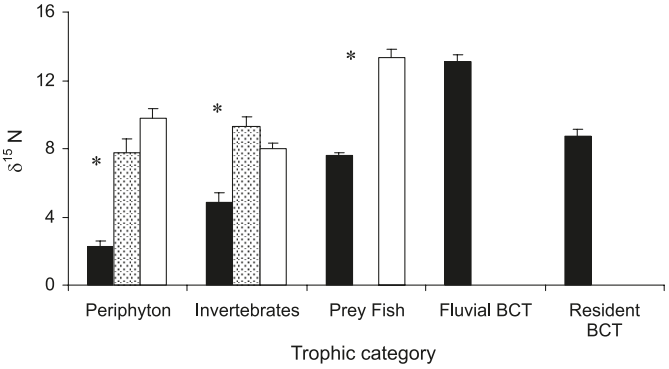
Prey fishes

In Bear River, we sampled $\delta^{15}N$ values from carp ($n = 3$), green sunfish ($n = 3$), redside shiner ($n = 3$), speckled dace ($n = 3$), and yellow perch ($n = 3$). In Hobble Creek, we sampled mountain sucker ($n = 2$), mountain whitefish ($n = 3$), and sculpin ($n = 3$). Prey fish $\delta^{15}N$ values in Bear River were 5.7‰ greater than in Hobble Creek (two-sample *t* test: $t_{[22]} = 3.80$, $P = 0.001$).

Discussion

This study contributes to the growing literature identifying uses of stable isotopes as markers of animal movement and human impacts in aquatic ecosystems (e.g., Harrington et al. 1998; Harvey and Kitchell 2000; Kennedy et al. 2005). Our results demonstrate the potential use of $\delta^{15}N$ as a marker of LDMs in landscapes with different land use. We compared $\delta^{15}N$ values and diets of fluvial BCT that migrate between forested, headwater reaches and lower elevation, mainstem reaches draining agricultural lands with $\delta^{15}N$

Fig. 4. . The δ^{15}N values (±2 standard error, SE) of periphyton, aquatic macroinvertebrates, and prey fish collected in Hobble Creek (solid bars), Smiths Fork (stippled bars), and Thomas Fork of Bear River (open bars) in July 2006. Fluvial and resident Bonneville cutthroat trout (BCT) mean δ^{15}N values from 2005 and 2006 samples from Hobble Creek are also shown for comparison. No prey fish were collected in Smiths Fork. Standard error bars do not extend past the symbol for each prey category. Locations in which Hobble Creek has significantly lower δ^{15}N values ($P < 0.05$) are marked with an asterisk (*).



values of resident fishes in headwater reaches. We found that fluvial BCT δ^{15}N was ≈4‰ greater than resident δ^{15}N, even though these fish had similar diets in headwater reaches. We compared δ^{15}N values of multiple trophic levels between impacted lowland and pristine headwater sites and found that δ^{15}N was 3.1‰–7.5‰ greater in lowland, mainstem reaches draining agricultural lands than in pristine, headwater reaches. We suggest that fluvial BCT δ^{15}N values reflect exposure to increased N inputs related to agricultural land use and trophic-level diet shifts while foraging in mainstem reaches.

Previous studies have used stable isotope analyses to differentiate among anadromous and nonanadromous individuals (Doucett et al. 1999*b*), to identify rearing habitats (Harrington et al. 1998; Kennedy et al. 2005), and to describe anadromous migration patterns (Kennedy et al. 2002). However, we are unaware of other studies that have used isotopic signatures in nonlethal tissue samples to differentiate among migratory and resident behaviors in an inland native trout population.

Relationship between *A. imperator* and life history

We found a large difference in infection rates among resident fishes in upstream vs downstream habitats. Our trap results support our hypothesis that fish become infected while in mainstem, lower-elevation habitats (i.e., Bear River and lower mainstem Thomas Fork and Smiths Fork) and further support our use of *A. imperator* as a marker of fluvial BCT fish that have recently spent time in these habitats.

Relationship between δ^{15}N, life history, and size

Stable isotope ratios in fish change as a result of size-constrained diet shifts (Kennedy et al. 2002), foraging location (Hansson et al. 1997; Harrington et al. 1998), and growth rate (Hesslein et al. 1993; Maruyama et al. 2001). We suggest that diet shifts and downstream foraging location drove the large difference between fluvial and resident BCT δ^{15}N values. However, our interpretation was confounded by the binomial size distribution of our samples — fluvial BCT were always larger than resident BCT. The positive correlation between predator size and prey size is well established in gape-limited fish (Mittlebach 1986) such as BCT and BNT (McHugh et al. 2007). Larger fish can feed on higher trophic levels, and δ^{15}N increases with trophic level within a food web (reviewed in McCutchen et al. 2003). Previous salmonid studies have found a positive correlation between fish size and δ^{15}N (Harrington et al. 1998; McHugh et al. 2007). We offer three lines of evidence to suggest that fish life history, not fish size, drives large δ^{15}N differences in our study system.

First, we used ANCOVA with fish size as a continuous covariate and found that fish life history was a significant predictor of δ^{15}N values. Second, we used cluster analysis to compare use of δ^{15}N and use of fish size as predictors of life history. We found that use of δ^{15}N had fewer missed assignments than fish size. Finally, we found that similar-sized fluvial BCT and resident BNT (>350 mm) sampled in upstream tributaries had similar diets but different δ^{15}N values. Stomach contents of these fishes were dominated by stream invertebrates, but BNT had greater *%N* and %IRI of piscivory than fluvial BCT. Nevertheless, fluvial BCT had significantly greater δ^{15}N than these BNT. This result stands in contrast to research examining stable isotopes and diet of similar-sized resident BCT and resident BNT in a neighboring watershed, where McHugh et al. (2007) found that BNT δ^{15}N was greater than or equal to BCT δ^{15}N for small, intermediate, and large fish. Maximum BNT δ^{15}N values were similar in both studies (10.63 and 10.5); however, McHugh et al. (2007) sampled no BNT larger than 320 mm. In addition, they compared BCT and BNT stomach contents and also found a higher occurrence of piscivory in BNT. Based on the stable isotope and stomach content results from our study and McHugh et al. (2007), we suggest that the large BNT δ^{15}N represents the local maximum for resident fishes and that values above this level are indicative of fluvial fish.

Stable isotopes and stomach contents

We used stomach content analyses in concert with stable isotopes to test whether fluvial BCT δ^{15}N signatures were acquired in lower-elevation mainstem habitats or headwater habitats. Multiple local factors can increase δ^{15}N, including trophic diet shifts, starvation, and growth rate. We found that fluvial BCT were not primarily piscivorous while foraging in headwater habitats; they foraged on similar trophic levels to resident BCT and a lower trophic level than large BNT. Because N undergoes mass-dependent fractionation of 3‰–4‰ at each trophic level (Cabana and Rasmussen 1996), fluvial BCT would have to feed one to two trophic levels above resident BCT and large BNT to acquire such high δ^{15}N values. This scenario is unrealistic given the simple food webs that characterize headwater tributaries.

We suggest that the fluvial BCT δ^{15}N signature reflects food sources from downstream sections of the mainstem Bear River that are enriched as a result of agricultural pollution. The δ^{15}N of primary producers was ≈7.5‰ greater in downstream sections adjacent to agricultural catchments than in forested, upstream tributaries. Moreover, the higher

stream invertebrate and prey fish $\delta^{15}N$ at these downstream reaches suggest that N pollution from agricultural sources is taken up through the food web. Our primary producers, stream invertebrate, and prey fish $\delta^{15}N$ values reflect literature values of known agricultural pollutants, including soil nitrate (–2.0‰ to +9.0‰) and human and animal waste nitrate (+10.0‰ to +20.0‰) (reviewed in Harrington et al. 1998). Agricultural N pollution and trophic-level diet shifts may act together to increase fluvial BCT δ^{15} N levels.

We cannot rule out effects of fluvial BCT growth rate and starvation on $\delta^{15}N$ signature. Stable isotopes in fish muscle tissue are controlled by growth and tissue turnover (Hesslein et al. 1993). Thus, retention of $\delta^{15}N$ after fish migration is dependent on the amount of muscle mass accreted between the time that fish leave downstream habitats and the time that they arrive in upstream tributaries to spawn (Doucett et al. 1999*a*; Kennedy et al. 2002). In our system, fluvial fish return to upstream tributaries in spring (Colyer et al. 2005). We are confident that fluvial BCT $\delta^{15}N$ values sampled in Hobble Creek in early summer and midsummer characterize downstream habitats because $\delta^{15}N$ sampled from salmonid white muscle tissue has a turnover time of 5–20 weeks, depending on growth rate (Kennedy et al. 2005; Perga and Gerdeaux 2005). Our seasonal isotope comparisons and mark–recapture data (W.T. Colyer, unpublished data) indicate that fluvial fish had slow growth rates in upstream tributaries. We found small decreases in $\delta^{15}N$ values from early summer to midsummer, suggesting that BCT had accumulated little muscle mass from energy derived in upstream tributaries and that consumed energy was used for maintenance rather than growth. In addition, W.T. Colyer (unpublished data) recaptured 14 fluvial BCT with *A. imperator* in Hobble Creek and found little change in their length, mass, or body condition daily growth rates in summer 2005.

Sampled individuals with low growth rates may have been starved as a result of high metabolic and spawning costs or cessation of feeding during spawning migrations. Starved and fasting animals can have higher $\delta^{15}N$ due to catabolism of body protein (Hobson et al. 1993), but literature values do not explain the 3‰–4‰ difference in $\delta^{15}N$ that we observed between fluvial and resident BCT. Hobson et al. (1993) found that starved birds had a 1.5‰ increase in muscle tissue $\delta^{15}N$, whereas Doucett et al. (1999*a*) observed no difference in anadromous Atlantic salmon (*Salmo salar*) muscle tissue $\delta^{15}N$ sampled throughout their spawning migration. In addition, our stable isotope and stomach content analyses indicated that fluvial BCT fed while in upstream tributaries.

Application of $\delta^{15}N$ as a fluvial marker

Nitrogen stable isotope analysis is a powerful tool that has provided understanding about ecological processes that are difficult to observe and measure, such as competitive interactions (McHugh et al. 2007), stock discrimination (Kennedy et al. 2005), and site fidelity (Hansson et al. 1997). In this study, we demonstrated an additional use of N stable isotopes: identification of individuals that move long distances in a population with multiple movement strategies. Our approach is faster and less expensive than the use of other stable isotopes (Kennedy et al. 2005) and radiotelemetry (Colyer et al. 2005). It also provides a nonlethal alternative to otolith microchemistry, which increases the utility of our approach in studies of sensitive or threatened populations. Although our approach does not provide the detailed information about specific movements that could be obtained via direct methods such as telemetry, it is a relatively simple method for coarse evaluation of movement patterns within a population, information that is important for management and conservation of native fish populations. For example, management of imperiled native trout populations in western North America often requires evaluating trade-offs between barrier construction to prevent genetic and disease contamination and barrier removal to improve connectivity and restore metapopulation dynamics (Fausch et al. 2006; Peterson et al. 2008). Knowing the degree of isolation of target populations and whether or not migratory life histories are expressed (i.e., are LDMs present) will inform these decisions.

Comparisons of our results with those of previous studies suggest that N stable isotopes are best used as a complement rather than an alternative to other methods such as telemetry. Gray et al. (2004) found that $\delta^{15}N$ did not discriminate between slimy sculpin (*Cottus cognatus*) from New Brunswick stream reaches with different land uses because there was minimal difference in $\delta^{15}N$ among stream reaches. Our study was performed over a larger spatial scale (>100 km) and there were large contrasts in land-use patterns between upstream and downstream reaches. Furthermore, we used stomach content analyses to test stable isotope assumptions, and we selected study locations based on previous research that identified use of upstream and downstream river reaches by fluvial BCT (Schrank and Rahel 2004, 2006; Colyer et al. 2005).

Use of $\delta^{15}N$ to understand movement patterns may have broad application in stream networks and terrestrial landscapes because of natural processes and human land uses that produce a mosaic of N isotopic landscapes. Fishes and amphibians make landscape-scale movements in stream networks that are disturbed by N-enriching processes, such as forest fires (Gresswell 1999), timber harvest (Johnston and Frid 2002), mine tailings (Nelson et al. 1991), road activity (Wofford et al. 2005), and agriculture (Schrank and Rahel 2004). Likewise, terrestrial organisms, such as birds, move across landscapes with sewage treatment plants and agricultural fields (i.e., Hobson 1999; Guillemain et al. 2000). This technique may be especially useful in tracking movements between upland and lowland locations (Fausch et al. 2002) because human land use is often greater in lowland sites. Research that capitalizes on the mosaic of land uses to describe the flow of individuals across space can provide knowledge of the spatial structure of populations and will improve our ability to design viable ecological reserves.

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