Relationships between Water, Otolith, and Scale Chemistries of Westslope Cutthroat Trout from the Coeur d'Alene River, Idaho: The Potential Application of Hard-Part Chemistry to Describe Movements in Freshwater

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Abstract.—We quantified Mg:Ca, Mn:Ca, Sr:Ca, and Ba:Ca molar ratios from an area representing the summer 2000 growth season on otoliths and scales from 1-year-old westslope cutthroat trout *Oncorhyncus clarki lewisi* collected from three streams in the Coeur d'Alene River, Idaho, system. We also quantified Mg:Ca, Sr:Ca, and Ba:Ca molar ratios in the water during summer 2000 and used regressions to model the assimilation of the various ratios into the otoliths and scales. Otolith and scale chemistries were linearly related to the Sr:Ca and Ba:Ca ratios in the water. The partition coefficients for the Sr:Ca ratios in otoliths and scales are higher in this freshwater system than in experimental results from a saline environment; we attribute these differences to differences in the biology of saltwater and freshwater fish. In contrast, the Ba:Ca partition coefficients are similar between the two environments, suggesting that our estimates are representative of those for a wide range of concentrations, temperatures, salinities, and at least two families of fish. The Mg:Ca, Sr: Ca, and Ba:Ca ratios varied significantly in otoliths from the three streams and could be used to reclassify individual fish to the streams from which they were collected with 100% accuracy. The Mn:Ca, Sr:Ca, and Ba:Ca ratios varied significantly in scales from the three streams and could be used to classify individuals with 82% accuracy. Given the heterogeneity of basin geology, the stability of water chemistry, and the degree of discrimination noted for the three streams we sampled, we believe that examination of the elemental composition of fish otoliths and scales could be used to describe the movements of fish in this and similar freshwater systems. Further, the high correlation between the ratios in scales and those in otoliths suggests scales may offer a nonlethal sampling alternative.

Describing movement has been a central problem in the biology and management of stream fishes. The migrations between freshwater and saltwater exhibited by anadromous fishes are relatively well known (e.g., Groot and Margolis 1991), but the movements occurring within freshwaters are poorly understood (Gowan et al. 1994; Fausch and Young 1995; Northcote 1997). Because migration and dispersal are believed to be funda-

mental processes defining populations (Hanski and Gilpin 1997; Rieman and Dunham 2000), this is a central problem in conservation management.

Linking movements to the structure and distribution of habitats across whole networks of streams is an important challenge (Schlosser 1995; Fausch et al. 2002). Migration or the movement among spawning, growth, and refuge habitats is a common characteristic of fish life histories. These movements generally proceed from spawning and rearing habitats in tributary streams to river, lake, or ocean environments (where most growth, maturation, and overwintering occur), and back to the natal sites to reproduce. Broad classifications of life history have been based on the scope and na-

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ture of these migrations (e.g., Northcote 1997), but tremendous variability may exist within and among species and populations. Arguably, that diversity influences the resilience and productivity of populations in varying environments (Healey 1991; Thorpe 1994; Tilman et al. 1994; Rieman and Clayton 1997).

The movement of individuals among local populations to reproduce, often termed dispersal (Howard 1960; Rieman and Dunham 2000) or reproductive ranging (Dingle 1996), also is important. One mechanism for dispersal is the straying of adults that fail to return to their natal habitats (Rieman and Dunham 2000), although other processes could be important (Hanski and Simberloff 1997). Movements among local populations, dispersal and subsequent gene flow, and the selective pressures associated with distinct environments are believed to be the primary forces structuring stream-fish populations (e.g., Quinn and Unwin 1993; Hendry et al. 2000; Quinn et al. 2000). Such movements may be critical to long-term persistence by linking local populations that independently would be vulnerable to extinction or by refounding those that do go extinct (Andrewartha and Birch 1954; Schlosser and Angermeier 1995; Hanski and Simberloff 1997; LePage and Cury 1997; Rieman and Dunham 2000; Rieman and Allendorf 2001).

Despite the potential significance of movement, we know relatively little about how it varies within and among populations of many fish species (e.g., Quinn 1993; Gowan et al. 1994). Migration patterns have been studied by tagging and recovering individual fish (e.g., Bjornn and Mallet 1964) or by tracking with radio or sonic transmitters (e.g., Swanberg 1997). Estimates of straying and gene flow have been made through indirect methods based on population genetics and directly through tag recovery studies. Because these methods have important but different limitations, comparisons are critical (Labelle 1992; Tallman and Healey 1994; Thompson and Goodman 1997; Wenburg and Bentzen 2001). Unfortunately, direct estimates of movement based on tagging are often very difficult to make. Because life history patterns may be highly variable (Willson 1997) and because significant dispersal may be the result of rare events (LePage and Cury 1997), very large numbers of marked individuals are required to detect or estimate movements with any precision (Seber 1982).

Passive chemical marks associated with the distinctly different environments fish encounter through life may provide a solution. Trace element analyses of otoliths and scales have proven to be effective for retrospectively describing the environmental history of individual fish as well as metapopulation dynamics (e.g., Rieman et al. 1994; Wells et al. 2000b; Thorrold et al. 2001). These techniques have been validated independently through controlled experimentation and field collections (Kalish 1991; Thorrold et al. 1998; Bath et al. 2000; Wells et al. 2000a, 2000b). However, except for a small number of studies (e.g., van Coillie and Rousseau 1974; Bronte et al. 1996; Kennedy et al. 2000, 2002), the work has concentrated on estuarine and marine waters, where one would expect great geographic variation in solute concentrations. Kennedy et al. (2000, 2002) have recently shown that stable isotope analysis of otoliths may have considerable potential for resolving movements in freshwater systems. However, in a system in which the geographic variation in isotopic ratio values is limited, it may be necessary to examine a suite of chemical markers. Our interest, then, was to adapt methods that have been established for marine and diadromous applications to describe fish movements wholly within freshwaters.

We conducted initial work on this problem in the Coeur d'Alene River basin of northern Idaho. Synoptic water sampling and geological mapping showed that important differences in water chemistry could exist among the streams in this basin. In this system, westslope cutthroat trout *Oncorhyncus clarki lewisi* is the dominant salmonid. Past work suggests that both resident (i.e., remaining in their natal streams throughout life) and migratory forms of cutthroat trout exist and that movements among streams may be important to the persistence of local populations (McIntyre and Rieman 1995). Our objectives were (1) to associate the chemistries of the otoliths and scales of juvenile fish with those of their natal streams; (2) to quantify the variation within and compare the results between these two hard parts; and (3) to evaluate the potential application of hard-part chemistry for describing fish movements in a freshwater river basin. In this study, we quantify the variation of element signatures of immature fish from three independent streams and evaluate their potential for describing movements in the Coeur d'Alene River system. Our work indicates that element analysis of hard parts could serve to address some of the more daunting tasks of describing movements within the freshwater environment. Further, scale analysis may offer a nonlethal sampling approach.

1.	Buckskin	10.	Big Hank	19.	Graham	28.	Bottom
2.	Jordan	11.	Flat	20.	Coal Corner	29.	Hudlow
3.	Sho	12.	Svee	21.	Scott	30.	West Fork Hudlow
4.	Lost Fork	13.	Yellow Dog	22.	Copper	31.	Middle Fork Hudlow
5.	Little Elk	14.	Lost	23.	Canyon	32.	Iron
6.	Halsey	15.	Cascade Gulch	24.	Skookum	33.	Tom Lavin
7.	Bear	16.	Cascade Gulch	25.	Deception	34.	Cedar
8.	Brett	17.	Brown	26.	Burnt Cabin	35.	Wolf Lodge
9.	Miners	18.	Grizzly	27.	Lone Cabin	36.	Marie

FIGURE 1.—Map showing the locations of the streams examined in this study. Dissolved Mg, Ca, Sr, and Ba levels were estimated for 36 streams in the Coeur d'Alene River basin in northern Idaho. One-year-old westslope cutthroat trout were collected from Miners (9), Yellow Dog (13), and Graham creeks (19).

Methods

Site description.—The Coeur d'Alene River is in the upper Columbia River basin near the Idaho–Montana border (Figure 1). This study includes fish and water samples from the Coeur d'Alene River, North Fork of the Coeur d'Alene River, and a small group of streams that feed into the northern portion of Coeur d'Alene Lake. The geology of the Coeur d'Alene River basin is characterized by a heterogeneous arrangement of Precambrian metasedimentary rocks (Lewis and Derkey 1999; Lewis et al. 1999; Miller et al. 1999) leading to substantial variation in stream water chemistry across the basin. We collected 1-year-old westslope cutthroat trout from three streams of the

Coeur d'Alene River system north of its confluence with the South Fork (from north to south, these streams were Miners, Yellow Dog, and Graham creeks; Figure 1). The lengths of these streams that are accessible to fish range from 5 to 8 km, and the low-flow wetted width is approximately 2–4 m for each stream. The hydrology is dominated by snowmelt, with peak flows in late spring and base flows in late summer and early fall.

Fish collection.—We used a backpack electroshocking unit (pulsed DC) to collect ten 1-year-old fish each from Miners (24–25 August 2000), Yellow Dog (16–17 August and 28 September 2000), and Graham creeks (26 July and 1 August 2000). We froze the fish until otoliths and scales

were removed with a stainless steel knife at the laboratory. Otoliths were stored dry in polyethylene vials, and scales were stored in paper collection envelopes.

Otolith and scale preparation.—We used a cautious cleaning procedure to be certain that the hard parts were free of loose and bound contamination. The otolith core was exposed following the methods in Rieman et al. (1994). We cleaned the otoliths and scales in a class 100 clean facility for laser ablation. All tools that came directly or indirectly into contact with the otoliths and scales were nonmetallic and acid washed. We triple-rinsed the otoliths with Millipore Milli-Q water, rinsed them for 1 min with ultrapure hydrogen peroxide (30%) to remove organics, sonicated them for 5 min in Milli-Q water, triple-rinsed them with Milli-Q water, and dried them under a laminar flow hood for 24 h. When possible, we prepared one nonregenerated scale from each fish. Scales were sonicated for 5 min in Milli-Q water, triple-rinsed with Milli-Q water, dried under a laminar flow hood for 24 h, and mounted with the distal side up on mounting tape for ablation. The isotopic intensities from the tape were similar to background levels for all isotopes quantified.

Elemental analysis of otoliths and scales.—Examination of the Coeur d'Alene River stream water chemistry showed that Sr, Ba, and Mg vary across the basin. Each of these elements replaces Ca in the hard-part crystal lattice, suggesting that they remain stable as the fish moves between habitats (reviewed in Campana 1999). Therefore, we examined otoliths and scales for Mg, Ca, Sr, and Ba. Previous work has shown that the Mn levels in hard parts can also vary substantially across environments (Wells et al. 2000b; Thorrold et al. 2001). Therefore, in addition to those elements analyzed directly in the water, we quantified Mn in otoliths and scales.

We used a Finnigan MAT Element 2 inductively coupled plasma mass spectrometer equipped with an ultraviolet (266-nm) Nd: YAG Merchantek LUV-266X laser ablation system to analyze otoliths and scales. From otoliths we ablated a raster from the area distal to the last annulus toward the edge representing approximately one-half of the summer growth period (spot size = 30 μm, pass = 60 s, frequency = 10, power = 30–50%, raster = 100 μm × 100 μm). From scales we ablated a raster from the edge of the scale toward the core representing a similar growth period as that ablated from otoliths (spot size = 10 μm, pass = 60 s, frequency = 10, power = 20%, raster = 100 μm

× 100 μm). We ran blanks and standards every ninth analysis to adjust for possible drift. The ablated material was swept by a carrier gas (Ar) into a dual-inlet quartz spray chamber. The Ar stream was then mixed with a wet aerosol (1% HNO_3) from a 20-μL/min PFA self-aspirating nebulizer. Five isotopes were quantified (^{25}Mg, ^{48}Ca, ^{55}Mn, ^{86}Sr, and ^{138}Ba). Liquid standards were introduced every nine samples through the nebulizer to account for instrument drift and changes in mass bias, with quantification following the procedure outlined by Rosenthal et al. (1999). This methodology alleviated the need for matrix matching with solid reference standards. The limits of detection were calculated as the mean blank values plus three standard deviations. Isotopic counts were converted to elemental intensities by multiplying by the percent natural occurrence of the isotopes. All data were standardized to Ca to account for the variability in laser energy and weight of ablated material and were converted to molar ratios.

Data analysis.—Weighted least-squares regressions, which correct for biases associated with heteroscedasticity, were used to quantify the relationships between water and hard-part chemistries. Also, partition coefficients, the molar ratio of the element in question to Ca in the hard-part relative to that in the water (McIntire 1963), were calculated. This ratio is an approximation of the slope from a linear regression in which the intercept is zero.

One-way analyses of variance (ANOVAs) were used to test for significant (α = 0.05) differences in trace element concentrations in hard parts among streams. Tukey's Studentized multiple range tests were used to evaluate differences in the hard-part chemistries from the three streams. Elements that varied significantly were entered into a multivariate analysis of variance (MANOVA) and canonical discriminant analysis (CANDISC procedure of SAS; SAS 1989) to characterize the multivariate elemental signatures of the hard parts. All MANOVA significance tests used Pillai's Trace statistic. Bootstrapped confidence ellipses were calculated around the class means of the first two canonical variates to locate significant differences in hard-part chemistries among streams. Finally, linear discriminant function analysis (LDFA) was used to quantify the accuracy of the classification of individuals to their resident streams based on the elemental signatures of the hard parts. The cross-validation algorithm of SAS (the DISCRIM procedure), which employs a jack-

knife technique, was used to determine classification accuracy. To meet the assumptions of homogeneity of variance and normal distribution of errors, all element : Ca values were $\log_e$ transformed for univariate and multivariate statistics.

Water collection and analyses.—During 10–12 July 2000, we sampled 36 natal streams in the Coeur d'Alene River basin to characterize dissolved Mg, Ca, Sr, and Ba concentrations (Figure 1). In the field, we vacuum-filtered 100 mL of water through a 0.45-µm membrane that had been prewashed with distilled water. We then acidified the samples to a pH of less than 1 with 1 mL ultrapure nitric acid for preservation. Two samples were taken at each site and the results averaged for all analyses presented herein. Multiple sites at Cedar and Wolf Lodge creeks and three branches of Hudlow Creek were sampled to evaluate the influence of local variation. Samples were then refrigerated until analysis. Temperatures at time of collection were also recorded.

All of the water analyses presented in this work were done with a Fison's Instruments Accuris inductively coupled plasma (ICP) optical emission spectrometer. The analytical wavelengths used for Mg, Ca, Sr, and Ba were 279.08, 317.93, 407.77, and 455.40 nm, respectively. Three on-peak integrations with 10-s intervals and one off-peak integration were used. The internal calibration standards were certified ICP single-element standards. Calibration standards and blanks were run every 15 samples.

The potential of these methods in the basin.—We quantified the temporal elemental variation in the Coeur d'Alene River system because seasonal variation in stream chemistry over the time frame represented by quantified hard-part chemistry could result in greater within-stream variation and thus reduce the classification accuracy of fish across streams. To evaluate seasonal variability, we compared the Sr:Ca and Mg:Ca ratios from samples in six streams (including Graham and Miners creeks) obtained in July 2000 with those obtained on 10 October or 11 November 2000. To evaluate the interannual variation in stream water chemistry, which is relevant to the application of hard-part chemistry methods across cohorts (e.g., Gillanders 2002), we compared Sr:Ca and Mg:Ca ratios for 16 streams obtained in July 2000 with those obtained in August 1999 (including ones from Yellow Dog and Graham creeks). The temporal stability of the Ba:Ca ratio was not evaluated because it was only assayed for July 2000 stream samples. We used the slopes of the temporal re-

lationships to evaluate the between-stream stability of water chemistry and the intercepts to evaluate system shifts. While the slopes and intercepts of these regressions are not independent of one another, this analysis yields a reasonable interpretation of the trends. Specifically, slopes not equal to 1.0 could indicate temporal variation in the relationship of stream chemistries to one another, and an intercept not equal zero could indicate a system shift in elemental concentrations.

We estimated the potential variation of hard-part chemistry signatures among streams across the system by comparing our ability to discriminate hard parts from three streams with the differences in water chemistry observed among our sample of 38 stream sites. First, stream element : Ca values were standardized to a mean of zero and variance of 1.0. Next, we used a nearest-neighbor cluster analysis (CLUSTER procedure of SAS) on the standardized stream chemistries to build similarity dendrograms. The results from the LDFA on fish from Miners, Yellow Dog, and Graham creeks were used as a benchmark to evaluate the significance of stream chemistry groupings and define the potential resolution of fish origin discrimination. Specifically, the classification accuracy of fish of known origin by means of hard-part chemistry (which was directly and linearly related to water chemistry) was used to define the minimum expected resolution of fish origin determinations across the system. As an illustration of the approach, consider fish from two streams that separate from each other by some minimum distance between clusters based on the stream chemistries. If fish from those streams can be clearly discriminated by the related hard-part chemistries, one can conclude that it would be possible to discriminate fish origins among other streams with similar or larger differences in stream chemistries.

Results

Otolith and Scale Relationships to Water Chemistry

Nonregenerated scales were not available for five fish (three from Miners Creek and two from Yellow Dog Creek), and two scales from Miners Creek fish yielded [86]Sr intensities about three standard deviations from mean background levels. We removed these two fish, which could have led to a slightly inflated estimated mean Sr:Ca value for scales from Miners Creek.

Otolith ($N = 30$) and scale ($N = 23$) chemistries were related to water chemistry (Figures 2, 3).
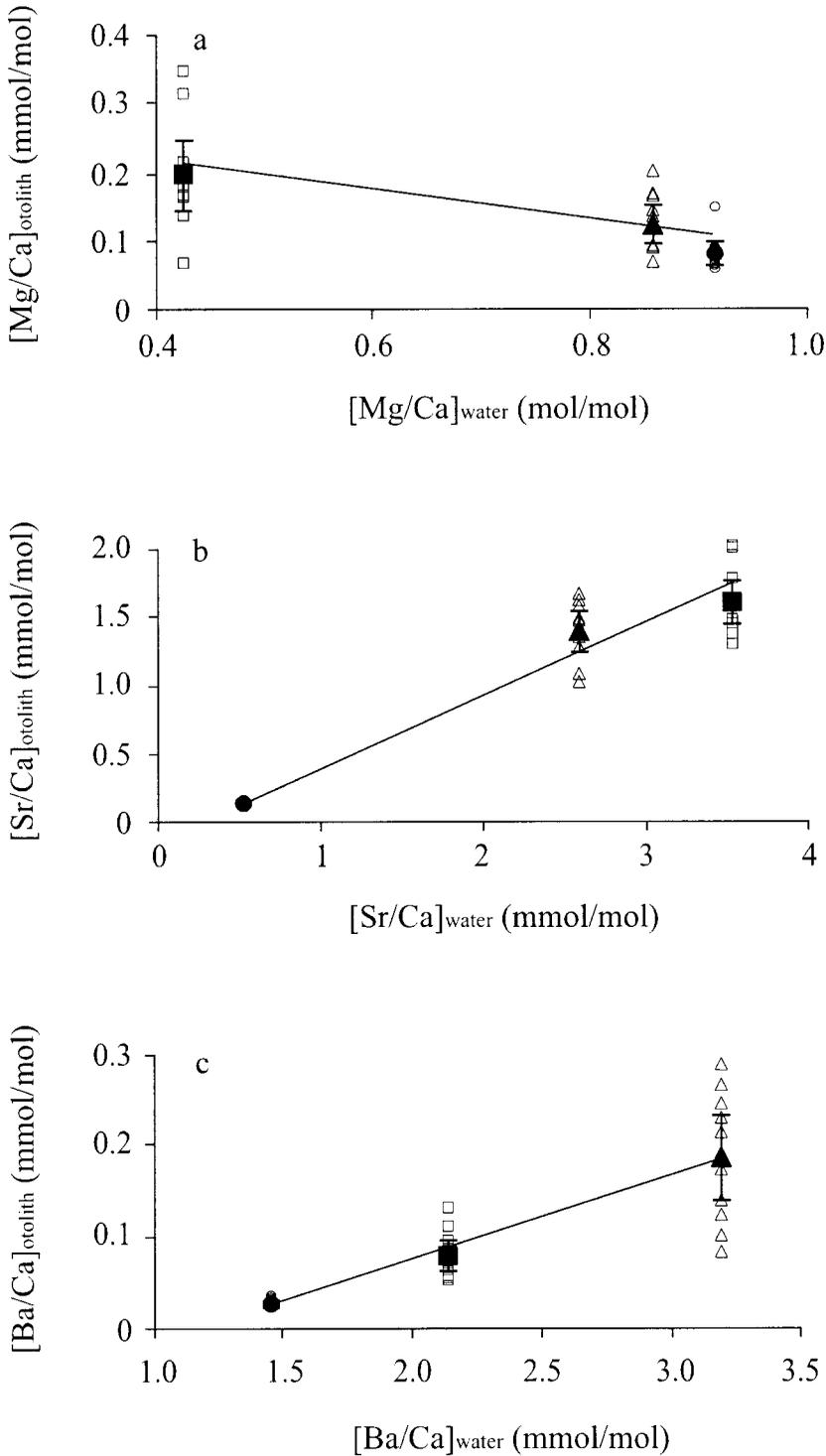
FIGURE 2.—Weighted least-squares regressions estimated from individual westslope cutthroat trout collected from Miners (open circles), Yellow Dog (open triangles), and Graham creeks (open squares) of the **(a)** Mg:Ca, **(b)** Sr:Ca, and **(c)** Ba:Ca ratios in otoliths on those in the water. Filled symbols represent average otolith values for each stream (±2 SEs).

Otolith chemistry was linearly related to the Mg:Ca, Sr:Ca, and Ba:Ca ratios of the water. Specifically,

$$[Mg:Ca]_{otolith}$$

$$= (-0.0002 \pm 0.00005SE) \cdot [Mg:Ca]_{water}$$

$$+ (0.30 \pm 0.5SE)$$

$$(r^2 = 0.39, P = 0.0003),$$

$$[Sr:Ca]_{otolith}$$

$$= (0.55 \pm 0.02SE) \cdot [Sr:Ca]_{water}$$

$$- (0.18 \pm 0.03SE)$$

$$(r^2 = 0.96, P = 0.0001), \quad and$$

$$[Ba:Ca]_{otolith}$$

$$= (0.09 \pm 0.01SE) \cdot [Ba:Ca]_{water}$$

$$- (0.10 \pm 0.02SE)$$

$$(r^2 = 0.71, P = 0.0001).$$

Scale chemistry was linearly related to the Sr:Ca and Ba:Ca ratios in the water (Figure 3). The relationships were

$$[Sr:Ca]_{scale}$$

$$= (0.39 \pm 0.03SE) \cdot [Sr:Ca]_{water}$$

$$- (0.06 + 0.06SE)$$

$$(r^2 = 0.88, P = 0.0001) \quad and$$

$$[Ba:Ca]_{scale}$$

$$= (0.32 \pm 0.07SE) \cdot [Ba:Ca]_{water}$$

$$- (0.22 + 0.15SE)$$

$$(r^2 = 0.50, P = 0.0002).$$

There was not a significant relationship between the Mg:Ca ratio in the water and that in scales.

The partition coefficients for the Sr:Ca ratio were calculated as 0.40 ($N = 30$; SE = 0.028) and 0.34 ($N = 23$; SE = 0.023) for otoliths and scales, respectively. Those for the Ba:Ca ratio were calculated as 0.04 ($N = 30$; SE = 0.004) and 0.22 ($N = 23$; SE = 0.020) for otoliths and scales, respectively, and that for the Mg:Ca ratio as 0.0002 ($N = 30$; SE = 0.00004) for otoliths.

Variation of Otolith and Scale Chemistries

There were significant differences in the otolith and scale chemistries from the three streams (Table
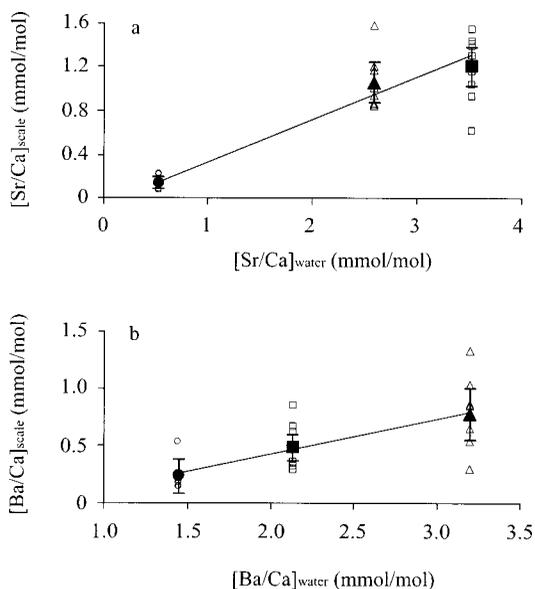
FIGURE 3.—Weighted least-squares regressions estimated from individual westslope cutthroat trout collected from Miners (open circles), Yellow Dog (open triangles), and Graham creeks (open squares) of the **(a)** Sr:Ca and **(b)** Ba:Ca ratios in scales on those in the water. Filled symbols represent average scale values for each stream (± 2 SEs).

1). Log$_e$ transformed Sr:Ca (ANOVA: $F = 1,049.17$; df = 27, 2; $P < 0.0001$), Ba:Ca ($F = 85.89$; df = 27, 2; $P < 0.0001$), and Mg:Ca ratios ($F = 12.78$; df = 27, 2; $P = 0.0001$) in otoliths varied significantly among streams (Table 1). The Mn:Ca ratios in otoliths did not vary significantly among streams. Log$_e$ transformed Sr:Ca ($F = 79.38$; df = 20, 2; $P < 0.0001$), Ba:Ca ($F = 13.14$; df = 20, 2; $P < 0.0002$), and Mn:Ca ratios ($F = 7.97$; df = 20, 2; $P = 0.0029$) in scales also varied significantly (Table 1). The Mg:Ca ratios were not significantly different among streams. The Pearson's correlation coefficient for individual otolith and scale Sr:Ca ratios was 0.82 ($N = 23$; $P = 0.0001$) and that for Ba:Ca ratios was 0.74 ($N = 23$; $P = 0.0001$; Figure 4). The Mg:Ca and Mn:Ca ratios were not correlated between hard parts.

The among-stream variation in hard-part chemistries could not be attributed to variation in temperature or fish growth. July 2000 point estimates of temperature were similar among Miners, Yellow Dog, and Graham creeks (10.5–11.9°C). The total lengths of fish collected from Miners Creek were slightly less than those of fish from the other streams ($F = 3.52$; df = 27, 2; $P = 0.044$; Table 1), but given the clear differences we observed in

TABLE 1.—Sample size (*N*) and mean total length (TL [mm]) of westslope cutthroat trout from Miners, Yellow Dog, and Graham creeks, Idaho, along with the Mg:Ca (mmol/mol), Mn:Ca (μmol/mol), Sr:Ca (mmol/mol), and Ba:Ca (mmol/mol) ratios in their otoliths and scales. Values in parentheses are standard errors. Tukey's Studentized multiple-range tests were used to evaluate differences in means; values without a letter in common are significantly (*P* < 0.05) different.

			Ratio			
Stream	*N*	TL	Mg:Ca	Mn:Ca	Sr:Ca	Ba:Ca
			Otolith chemistry			
Miners	10	82.3 (3.30) z	0.08 (0.008) z	9.00 (0.476) z	0.12 (0.004) z	0.03 (0.016) z
Yellow Dog	10	96.6 (4.86) y	0.12 (0.014) z	8.46 (0.705) z	1.40 (0.069) y	0.19 (0.023) x
Graham	10	89.1 (3.10) zy	0.20 (0.026) y	7.33 (0.469) z	1.61 (0.079) y	0.08 (0.008) y
			Scale chemistry			
Miners	5	87.4 (4.48) z	23.25 (5.881) z	144.00 (8.716) z	0.14 (0.034) z	0.23 (0.074) z
Yellow Dog	8	100.4 (5.27) z	26.42 (5.528) z	253.91 (34.880) zy	1.06 (0.088) y	0.78 (0.111) y
Graham	10	89.1 (3.10) z	31.70 (4.073) z	326.58 (36.192) y	1.20 (0.088) y	0.48 (0.058) y
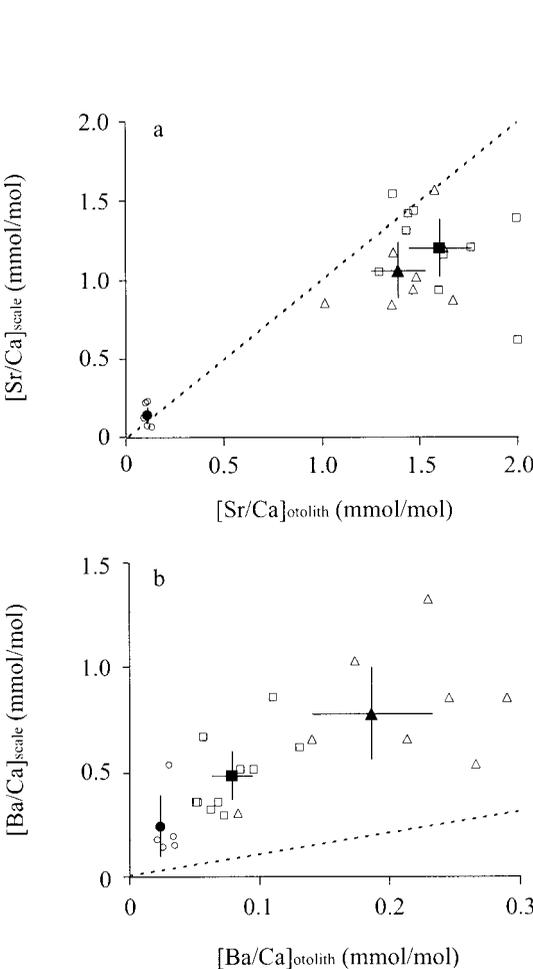
FIGURE 4.—**(a)** Sr:Ca and **(b)** Ba:Ca ratios in scales plotted against those in otoliths for Miners (open circles), Yellow Dog (open triangles), and Graham creeks (open squares). Filled symbols represent average scale-to-otolith values for each stream (±2 SEs); dashed lines indicate equivalence.

hard-part chemistries among the streams, we believe that the minor differences in size had little to do with those in hard-part chemistries.

Both otoliths and scales provided stream-specific element signatures. The results from a MANOVA demonstrated that otolith signatures, as defined by $\log_e$ transformed Sr:Ca, Ba:Ca, and Mg:Ca ratios, varied significantly among streams (Pillai's Trace = 1.69; df = 6, 52; *F* = 47.12; *P* < 0.0001). Scales from the three streams also had significantly different signatures with $\log_e$ transformed Sr:Ca, Ba:Ca, and Mn:Ca ratios as the dependent variables (Pillai's Trace = 1.22; df = 6, 38; *F* = 9.88; *P* < 0.0001). Further, bootstrapped 95% confidence intervals around the class means of the first two canonical variates did not overlap for otoliths or scales (Figure 5). The Sr:Ca ratio was weighted most heavily for the first canonical variate and the Ba:Ca ratio most heavily for the second canonical variate for both otoliths and scales. The LDFA demonstrated that otolith chemistry was distinct enough to classify individual fish to their resident stream with 100% accuracy (Table 2). Using scale chemistry, individuals were classified with 82% accuracy. All Miners Creek fish were classified correctly using either otolith or scale chemistry, but scale chemistry was less accurate for Yellow Dog (error = 25%) and Graham creeks (error = 30%; Table 2). Fish from Graham Creek were misclassified to Yellow Dog Creek and vice versa.

Stream Chemistries and Temperatures within the Coeur d'Alene River Basin

The Mg:Ca, Sr:Ca, and Ba:Ca ratios varied among the 38 stream sites assayed. That for Mg:Ca ranged from 0.31 to 1.03 mol/mol (mean = 0.66, median = 0.62, SE = 0.33), that for Sr:Ca
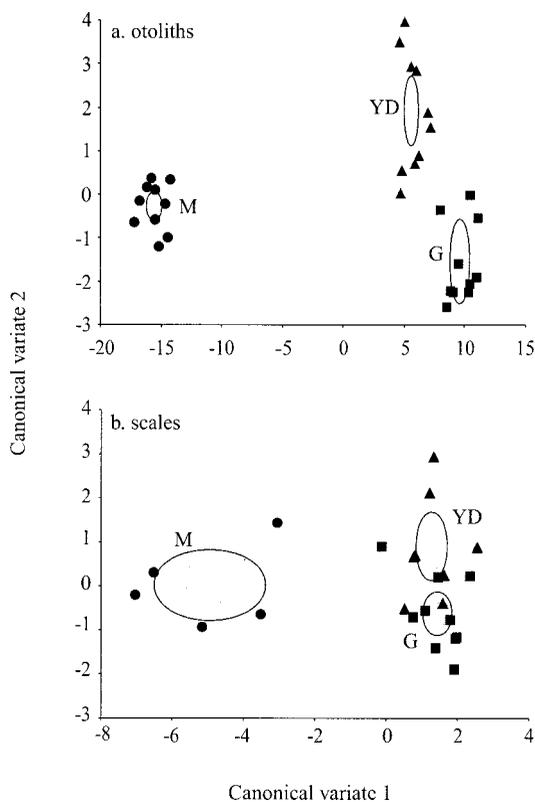
FIGURE 5.—Results of canonical discriminant analysis used to characterize differences in the multivariate elemental signatures of **(a)** otoliths and **(b)** scales of westslope cutthroat trout from Miners (M; circles), Yellow Dog (YD; triangles), and Graham creeks (G; squares). Shown are individual canonical coefficients for canonical variates 1 and 2. Shaded areas are bootstrapped 95% confidence ellipses around the class means, which demonstrate that there exist stream-specific elemental signatures.

TABLE 2.—Results of using linear discriminant function analysis to classify individual 1-year-old westslope cutthroat trout to the streams from which they were collected based on elemental signatures in their otoliths and scales. Values indicate the cross-validation accuracy using Mg:Ca, Sr:Ca, and Ba:Ca ratios to classify otoliths and Mn:Ca, Sr:Ca, and Ba:Ca ratios to classify scales.

		Assigned stream		
Source stream	N	Miners	Yellow Dog	Graham
Otolith cross-validation accuracy (%)				
Miners	10	100	0	0
Yellow Dog	10	0	100	0
Graham	10	0	0	100
Scale cross-validation accuracy (%)				
Miners	5	100	0	0
Yellow Dog	8	0	75	25
Graham	10	0	30	70

= 0.21, SE = 0.06, P = 0.006; Figure 6a). The Mg:Ca ratio was stable between summer and autumn both among streams (slope = 1.0, SE = 0.04, r^2 = 0.99) and as a system (intercept = −0.03, SE = 0.03, P > 0.05; Figure 6b). The Sr:Ca ratio among streams was relatively unaltered between years and through the growth season (Figure 6c, d). Regression analysis showed that there was an equivalent relationship between summer 2000 and summer 1999 stream Sr:Ca values (slope = 1.00, SE = 0.04, r^2 = 0.98), and there was no system shift (intercept = 0.07, SE = 0.10, P > 0.05; Figure 6c). Into autumn, the Sr:Ca ratio varied for some streams (slope = 0.88, SE = 0.01, t = 12, r^2 = 1.0), but there was only minimal shift in the system (intercept = 0.06, SE = 0.02, P = 0.02; Figure 6d).

Temperature differences across the 38 stream sites that we sampled will have little effect on among-stream variation in hard-part chemistry. Point estimates of temperature collected in July 2000 for the 36 streams, including the second sites for Cedar and Wolf Lodge creeks, had a range of 8.3°C but were generally similar across the system (N = 38, mean = 10.6°C, median = 10.5°C, SE = 0.30). Because there is significant diel variation in temperature, the minor differences that existed may have resulted from the timing of sample collection and would not be expected to influence hard-part chemistry in a sample of fish.

Potential Determination of Fish Origins

The cluster diagram for stream chemistries demonstrated that there was good potential to discriminate fish from various streams within the system (Figure 7). We judged the significance of the

from 0.54 to 6.14 mmol/mol (mean = 2.21, median = 1.61, SE = 0.24), and that for Ba:Ca from 0.29 to 5.11 mmol/mol (mean = 1.76, median = 1.69, SE = 0.17). Magnesium concentrations were highly correlated to those of Ca (r = 0.88, N = 38, P = 0.0001), yet the Mg:Ca ratio was not. Although Sr (r = 0.39, N = 38, P = 0.02) and Ba (r = 0.55, N = 38, P = 0.0004) were only weakly correlated to Ca, the Sr:Ca (r = −0.73, N = 38, P = 0.0001) and Ba:Ca ratios (r = −0.70, N = 38, P = 0.0001) were negatively correlated to Ca, indicating that increases in Ca across the system were not met with increases in Sr or Ba.

The Mg:Ca ratios among streams were variable between years (slope = 0.77, SE = 0.11, t = 2.09, r^2 = 0.77), and summer 2000 values were significantly greater than summer 1999 values (intercept

Annual variation   Seasonal variation

FIGURE 6.—Interannual and seasonal variation of the **(a)** and **(b)** Mg:Ca and **(c)** and **(d)** Sr:Ca ratios in water. Ratios were estimated for 16 streams during August 1999 and July 2000 as well as for 6 streams during fall 2000. Values on the equivalence line (dashed) were stable.

groupings based on the assignment of fish of known origin to Miners, Yellow Dog, and Graham creeks. Because we obtained 100% classification accuracy for fish from these streams using otolith chemistry, we expect to be able to discriminate fish origins from streams with similar or larger differences in water chemistry. If we assume that the node linking Yellow Dog and Miners creeks (Figure 7) represents the minimum distance between clusters (stream chemistries) that is necessary to discriminate the origins of individual fish (otolith chemistries), there are at least seven clusters of streams in the system that should be clearly discriminated.

The patterns detected in the cluster analysis followed the general patterns in lithology (Lewis and Derkey 1999; Lewis et al. 1999; Miller et al. 1999). For example, one cluster of nine streams was defined by the seven lithologic groups identified for the Wallace Formation (Figure 7a). Another cluster of 12 streams was

defined by the five lithologic groups identified for the Striped Peak Formation (Figure 7d, e combined). There was significant variation in stream chemistry at finer spatial scales as well. Lower and upper Wolf Lodge Creek grouped together, although upper and lower Cedar Creek and branches of the Hudlow Creek each grouped into different clusters (Figure 7).

Discussion

The chemistries of otoliths and scales hold promise as keys to clarify the movements of fish wholly within freshwaters such as the Coeur d'Alene River basin. We found substantial variation in water chemistry among and even within streams that was associated with a heterogeneous lithology. Those differences appear to be temporally stable and strongly associated with the chemistry of otoliths and scales of fish originating in those streams. Based on a conservative interpretation, otolith chemistry should allow the discrim-

ination of fish originating at sites from at least seven groups of stream chemistry. Finer resolution appears likely, but it will be necessary to sample fish from a subset of more chemically similar streams to determine precisely the minimum resolution possible. Large differences in geology and stream chemistry at the subwatershed scale might be used to distinguish fish movements within streams or between nearby streams.

Chemistry and Comparison of Scales and Otoliths

The ability of otolith analysis to resolve fish movements between chemically distinct environments has been well defined in previous research (e.g., Secor 1992; Limburg 1995; Secor and Piccoli 1996; Thorrold et al. 1997; Limburg 2001). Otoliths are chemically stable and thus provide an accurate permanent record of the environmental history for any individual fish (Campana 1999). The chemical properties of scales are less well defined. In our work, scale chemistries were more variable and the discrimination of known-origin fish was poorer than with otoliths. Scales may also be less stable. If scale microchemistry is to be used as a proxy for past environmental conditions, the material in scales must remain stable long enough to address the hypotheses at hand. There is evidence that scales may cease to grow or even be resorbed during times of physiological stress (Bilton and Robins 1971). Wells (2000) showed that elemental concentrations from the scales of weakfish *Cynoscion regalis* returning to spawn had been altered from the time the fish emigrated as juveniles from the estuarine nursery. One explanation for the alteration of the signatures offered by Wells (2000) was stress from the maturation process. During gonadal development Ca demand is relatively high (Mugiya and Watabe 1977; Kalish 1991), and experimentation has shown that injections of estradiol lead to the mobilization of Ca from the scale to the blood plasma more so than from other hard parts (Mugiya and Watabe 1977). A second explanation for the alteration of the scales' elemental signature was an extended crystallization process (Fouda 1979) that continued after the juveniles emigrated from their estuarine nursery grounds. The length of time required for the scale to complete the crystallization process in any given region on the scale has not been determined. Finally, the amount of mineral material available for analysis in scales is substantially less than that in otoliths (Fouda 1979). As a result, two scales from Miners Creek fish yielded [86]Sr inten-

sities approximately three standard deviations from mean background levels. Given the low Sr concentrations in some freshwater fish scales and the limited amount of mineral material available, we suggest that future researchers quantify the more abundant isotope [88]Sr.

The Sr:Ca and Ba:Ca ratios varied geographically for both otoliths and scales. There was also significant geographic variation in the Mg:Ca ratios in otoliths but in not scales. This finding was not unexpected. Given the integral role of Mg in the formation of apatite (Bigi et al. 1992), Wells et al. (2000b) suggested that Mg:Ca variation within the scale may exceed that between scales from different environments. The Mn:Ca ratios varied among the scales from the three streams but not among the otoliths. Because biogenic apatite has a high affinity for Mn (Wells et al. 2000b), the concentration in scales can be orders of magnitude higher than that in otoliths so that there would be a higher likelihood of significant variation across the river basin. Manganese was not assayed for the river basin, so we could not examine relationships between water and scale chemistry. Either way, Mn^{2+} has been found to be unstable in the aquatic environment (Wetzel 1983), so that point estimates may shed little light on the relationships.

The partition coefficients from this study can be compared with those from previous experiments to help understand the assimilation of elements into scales and otoliths. In this study, the partition coefficient of the Sr:Ca ratio was 0.40 for otoliths and 0.34 for scales. These values are double those from previous experiments with species in marine environments (e.g., Bath et al. 2000; Wells et al. 2000a). Bath et al. (2000) estimated the partition coefficient for the Sr:Ca ratio as 0.19 in otoliths, and Wells et al. (2000a) estimated it as 0.16 in the scales of spot *Leiostomus xanthurus* reared at 12–24 mmol/mol, 20° and 25°C, and a salinity of 20‰. Other marine species have similar assimilation rates for otoliths as those reported by Bath et al. (2000; Kalish 1991). Our results may reflect differences in Sr:Ca uptake between marine and freshwater environments. Marine fish obtain elements through the intestinal walls (Evans 1993; Campana 1999), while freshwater fish obtain them through chloride cell calcium channels in the gill (Evans 1993; Campana 1999; Katoh and Kaneko 2002). Unlike with Sr, the partition coefficients of the Ba:Ca ratios for otoliths and scales were similar to those determined from previous experiments. The estimated partition coefficients from this study were 0.04 for otoliths and 0.22 for
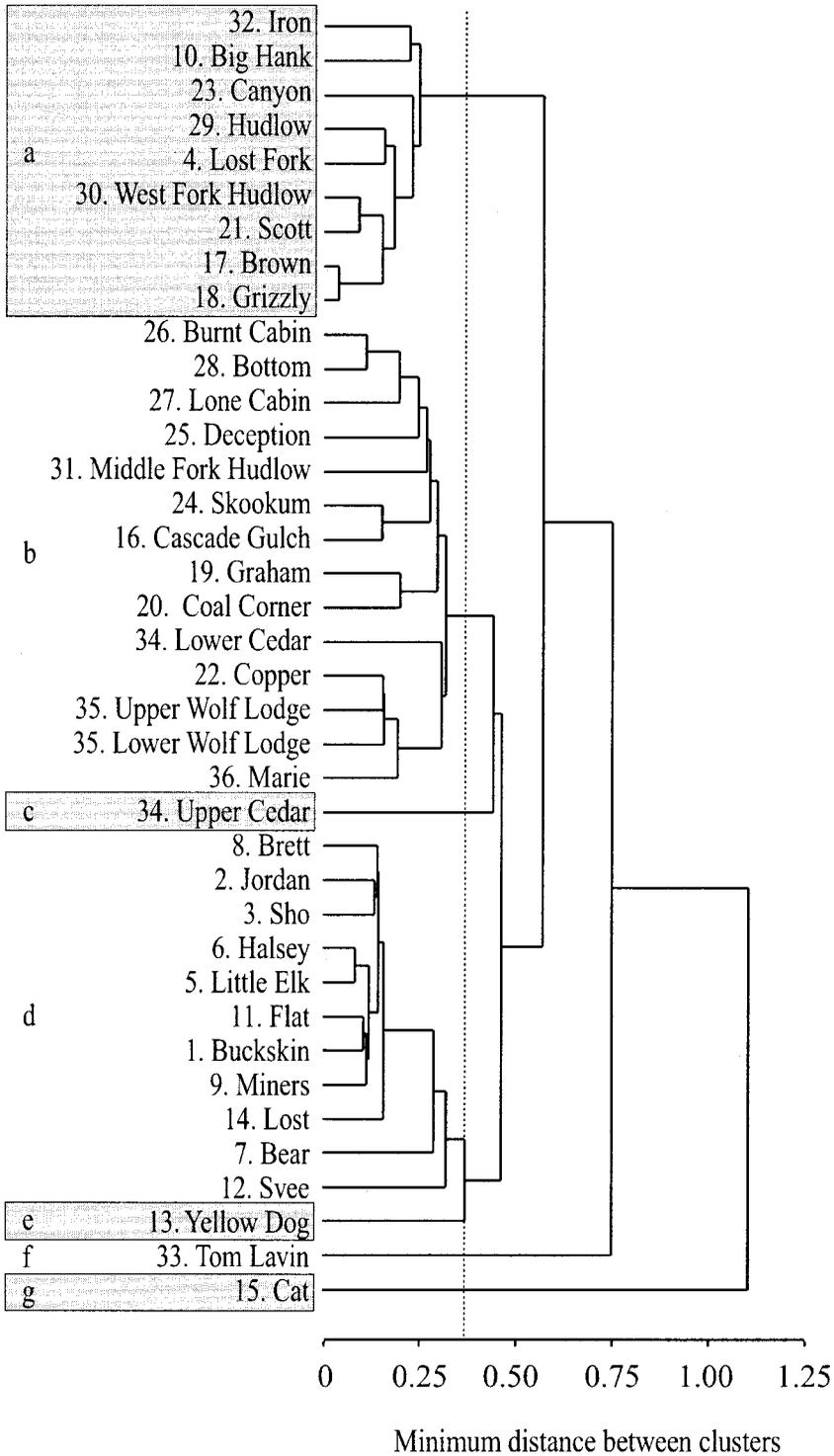
FIGURE 7.—Relationships among the 36 streams sampled in July 2000 using a nearest-neighbor cluster analysis on the standardized Mg:Ca, Sr:Ca, and Ba:Ca stream values. We defined seven groupings (a–g) based on our success in discriminating individual fish to Miners, Yellow Dog, and Graham creeks. The dotted vertical line represents the minimum distance used to define clusters. With each stream name is its number from Figure 1.

scales. Coefficients for experimentally reared spot were 0.06 for otoliths (Bath et al. 2000) and 0.20 for scales (Wells et al. 2000a). The partition coefficients for Ba:Ca water concentrations ranging from 0.15 to 3.2 mmol/mol appear to be consistent across families, water salinities, and temperatures.

There was a weak ($r^2 = 0.39$) but significant negative relationship between the Mg:Ca ratio in water and that in otoliths. This is counterintuitive and ultimately suggests that the highest concentration of Mg:Ca in the otolith will occur with the lowest concentration in stream water. It is possible that our least-squares regression is not indicative of the true relationship and instead is being driven by two points, specifically, Graham Creek and the combined effect of Yellow Dog and Miners creeks. It may be that one of these streams was an outlier. Interestingly, we noted a similar negative but insignificant relationship for scales. With our limited sample size and basin coverage, we cannot confirm any explanation for the negative relationship. The Mg:Ca ratio was the least influential ratio used for discriminating origins, and its absence from this analysis did not alter the results for the allocation of individuals to resident stream or those of our cluster analysis. Therefore, if the reported significance of our estimated slope is an error, it has little effect on our interpretation of the results. To determine the true relationship between Mg in water and hard parts, it may be necessary to run controlled experiments with growth rate (Sadovy and Severin 1994), temperature (Bath et al. 2000), and water hardness (Campana 1999) as potential factors.

Application and Limitations

The results of our work are consistent with those of other work demonstrating the utility of otolith microchemistry for resolving fish movements among chemically distinct environments (e.g., marine versus freshwater). Our work shows that it should be possible to extend the application within freshwaters and to streams within a single river basin. Scales show similar patterns to otoliths, but until more information is available, we believe that the use of scale chemistry will have limited application. At present, attempts to determine fish origins using scales will probably have to be restricted to immature fish that have spent a significant portion of time in their natal stream or to those that have moved from their natal stream shortly before capture.

The application of either hard part will require considerable care. It is apparent, for example, that relatively fine-scale variation in water chemistry could confound any analysis focused on larger-scale patterns. In systems with a geology as heterogeneous as that of the Coeur d'Alene River basin, each stream may show a different degree of local and large-scale variation and distribution in water chemistries. The collection of detailed chemistries for all potential stream environments will be important for the application of these methods. In this case it would be necessary to carefully define the spatial scale of the biological processes of interest in the context of the physical processes influencing water chemistry to be fully aware of the power and limitations of these methods for any prospective study (Schneider 1994).

It may be possible to determine likely fish origins by comparing hard-part chemistries directly with observed water chemistries that represent unique element : Ca ratios within the system (e.g., Tom Lavin and Cat creeks). However, within regions where element : Ca ratios are distributed more continuously, we may not yet be in a position to identify fish origins solely from quantified geographic variation in water chemistry. Biotic and abiotic interactions (reviewed in Campana 1999) may have subtle effects on the actual hard-part chemistries in fishes. Therefore, a conservative design should include the collection of fish from each potential environment. From these fish the researcher could develop a library of hard-part signatures for each potential environment. For any future sample for which place of origin is of interest, sample chemistries could be compared with those from the library of hypothetical sources to determine which is most likely.

Our findings demonstrate that in this freshwater system hard-part microchemistry can be used to determine the origins of individual fish. By taking advantage of the heterogeneity in water chemistry, as represented in hard parts, it could be possible to directly estimate dispersal and migration rates among adjacent streams. It should also be possible to evaluate the relative contribution of resident and migratory life histories (e.g., Rieman et al. 1994) in streams that differ in chemistry from the main-stem river or lake. Because scales represent a nonlethal sampling approach, many of the typical concerns of tag–recapture studies, including limited sample size and tagging mortality, might be avoided. Management applications might include estimates of life history diversity within and among streams or an evaluation of the relative contribution of different production areas to a population. Conceivably, these methods could help define es-

sential habitats and quantify the benefits of habitat restoration efforts.

Conclusions

This work provides a foundation for the application of otolith and scale chemistries to describe patterns of fish movement wholly within freshwater systems. Our work shows that otoliths can provide good resolution among streams with heterogeneous chemistry. It also suggests that scales may provide a nonlethal alternative to otolith analysis, but the limitations are greater than for otoliths. These observations are similar to those from previous studies that examined scale and otolith chemistries in marine environments (Wells et al. 2000a, 2000b; Gillanders 2001). The analysis of markers such as isotopic ratios (e.g., Thorrold et al. 1998; Kennedy et al. 2002) in combination with the elemental approach used here could substantially extend the range of systems in which these methods might be used. With any application, however, the results of a careful analysis of the sources and the scale of variation in water and hard-part chemistry should be considered in the study design to support the specific hypotheses of interest.

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