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Predicting strontium isotope variation and fish location with bedrock geology: Understanding the effects of geologic heterogeneity

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ABSTRACT

Recent advances in using naturally occurring isotopes to reconstruct movement patterns have revolutionized the study of migration and spatial patterns across taxa. Isoscape approaches utilize isotopic variation in the underlying geology to quantify migration pathways. Spatial patterns in the geology can be used to predict isotopic variation, such as $^{87}Sr/^{86}Sr$; however, previous attempts to create predictive models have had mixed results. Our primary objective was to investigate the relationship between bedrock lithology and $^{87}Sr/^{86}Sr$ ratio as a tool to extend the spatial resolution of animal migration studies. Secondly, we investigated the ability to use geologic prediction as an *a priori* tool for determining chemically distinct watersheds. We first developed a regression model to relate known stream water $^{87}Sr/^{86}Sr$ to rock information from geologic maps, then used model outputs to classify adult fall Chinook salmon to their juvenile rearing location from $^{87}Sr/^{86}Sr$ signatures recorded in their otoliths (ear bones). We discuss the effect of scale and geologic heterogeneity on our ability to determine $^{87}Sr/^{86}Sr$ ratios within the study area. Our results indicate that the relationship between $^{87}Sr/^{86}Sr$ values and bedrock lithology can be used to accurately determine the rearing location of fish using otolith $^{87}Sr/^{86}Sr$ signatures. The scale at which geology can be used as a predictor of $^{87}Sr/^{86}Sr$ values is constrained by geologic heterogeneity and inherent variability in $^{87}Sr/^{86}Sr$ ratios within major rock categories. Further, our results indicate that geological data alone can be used to quantitatively investigate which watersheds are likely to be distinguishable using this method within a basin. Geologic prediction also has the potential to improve the scale and resolution of isotopic studies and the development of isoscapes. By applying measures of spatial heterogeneity we will be better able to quantitatively place limits on the accuracy of geologic predictions of $^{87}Sr/^{86}Sr$ ratios.

1. Introduction

Recent advances in reconstructing location and movement patterns using naturally occurring isotopes have revolutionized the study of migration and spatial patterns of habitat use across taxa (Hobson et al., 2010). Isotopic methods have allowed researchers to link breeding and overwintering grounds of butterflies (Wassenaar and Hobson, 1998) and birds (Marra et al., 1998; Wassenaar and Hobson, 2000; Hobson et al., 2012), to quantify the natal origins and movement patterns of fish (Harrington et al., 1998; Thorrold et al., 1998; Kennedy et al., 2002; Hogan et al., 2007), whales and bats (Hobson, 1999), and to identify the forensic location of marijuana origin and growing conditions (Hurley et al., 2010). Recent investigations have reconstructed movement patterns in unprecedented temporal and spatial detail (1–10 km) (Hamann and Kennedy, 2012) and at larger regional scales (Barnett-Johnson et al., 2010) that would be impossible using traditional tagging techniques.

The precision and power of landscape isotope, or isoscape, approaches rely on the underlying isotopic variation in the landscape (West et al., 2010). The ratio of strontium isotopes ($^{87}Sr/^{86}Sr$) can exhibit fine scale environmental variation in river systems, making it useful in studying, origin, migration and species distribution at both large and small scales (Kennedy et al., 1997; West et al., 2009; Barnett-Johnson et al., 2010; Hamann and Kennedy, 2012; Muhlfeld et al., 2012). Also, in contrast to most other isotope systems, $^{87}Sr/^{86}Sr$ values are tightly linked to the underlying geology (Faure, 1977; Bain and Bacon, 1994; Stewart et al., 1998). This significant relationship between bedrock geology and watershed chemistry may allow stream water $^{87}Sr/^{86}Sr$ ratios to be directly predicted from geology, potentially leading to more accurate $^{87}Sr/^{86}Sr$ isoscapes and increasing the resolution and extent of research with less sampling effort. Lastly, because biological fractionation of Sr isotopes does not occur, a precise signature of provenance of organisms or habitat use is possible if water chemistry can be characterized or predicted (Graustein, 1989; Kennedy et al., 1997, 2000).

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Previous attempts to predict $^{87}Sr/^{86}Sr$ using geologic variation, both across the landscape and in surface water, have been met with varying degrees of success (Chesson et al., 2012). Humston et al. (2006) introduced a qualitative, *a priori* tool for researchers to determine the feasibility of isotopic and elemental studies within a study reach. Barnett-Johnson et al. (2008) reported that the majority of $^{87}Sr/^{86}Sr$ variation in the California Central Valley could be explained using felsic and old sedimentary rock within the basin but did not extend this predictive relationship to predict $^{87}Sr/^{86}Sr$ values within the basin or determine the location of salmon in the study. Bataille and Bowen (2012) created large scale isoscapes of $^{87}Sr/^{86}Sr$ values with landscape geology, age, and weathering rates which explained 70% of the variation in surface water $^{87}Sr/^{86}Sr$ across the United States. They then applied this model to Caribbean watersheds and extended it to include additional sources of $^{87}Sr/^{86}Sr$ (Bataille et al., 2012). While contributing to our understanding of spatial variation in Sr isotope signature, prior studies have been hampered by an inability to generalize predictions and difficulty in predicting across large differences in geologic makeup or spatial scale.

We hypothesize that understanding how geology varies across the landscape using metrics of landscape scale and heterogeneity will improve our ability to generalize isotopic predictions from bedrock geology in the future. We further hypothesize that geologic predictions can be used to increase the resolution and extent of migration studies, and that watershed geologic makeup alone can be used as an *a priori* tool to isolate landscapes that are conducive to such studies.

The objective of this paper is to investigate the feasibility of $^{87}Sr/^{86}Sr$ prediction from bedrock as a tool to extend the spatial resolution of animal migration studies. We first present a regression-based approach that relates surface water $^{87}Sr/^{86}Sr$ measurements to bedrock lithology in the Snake River basin of Idaho and Washington. We then demonstrate that outputs from this model can be used to correctly classify the location of juvenile salmon. Next, we apply our regression model to unsampled watersheds within the basin and discuss the effect of watershed scale and geologic heterogeneity in creating generalized predictions of $^{87}Sr/^{86}Sr$ prediction in the future. Finally, we analyze the geologic differences needed to distinguish watersheds isotopically and use geologic data alone as an *a priori* tool to determine the whether watersheds are likely to be isotopically distinct.

2. Methods

Our primary goal was to develop a statistical relationship between $^{87}Sr/^{86}Sr$ values within the Snake River basin and the associated bedrock geology to test whether it could be applied to answer ecological questions. Secondly, we examined this geologic relationship to determine under what geologic conditions and watershed scales this type of geologic modeling could be used to improve isoscape modeling of $^{87}Sr/^{86}Sr$ ratios.

To develop our geologic relationship we used water samples collected seasonally to measure dissolved $^{87}Sr/^{86}Sr$ isotope ratios from 13 sites throughout the Snake River basin by Hegg et al. (2013) as the dependent variable to create a multiple linear regression. All samples were analyzed using Thermal Ionization Mass Spectrometry and the seasonal values for each site were averaged. Refer to Hegg et al. (2013) for specific analysis methods. The primary rock types in the watershed upstream of each sample point were quantified and used as the independent variable (Table 1 in the Online Appendix).

This regression relationship was then applied to a recent dataset of fish otolith $^{87}Sr/^{86}Sr$ values to test whether it could be used to extend the resolution or scale of migration studies. To do this, a linear discriminate function was developed using the predicted outputs of our regression equation with the geology of watersheds within the Snake River basin as inputs. We used $^{87}Sr/^{86}Sr$ signatures of the rearing stage for 127 adult and juvenile salmon from Hegg et al. (2013) to test the performance of our regression relationship as a method for determining the rearing location of fish of fish. We used this fish dataset because the original classification had been completed using the same water samples as we used to create our regression relationship. Therefore, by comparing these two approaches, we can attribute any differences in classification accuracy to the effects of geologic prediction.

Understanding the scale at which geologic predictions can be made is important for developing future isoscape models. Therefore, we analyzed the ability of our regression model to determine $^{87}Sr/^{86}Sr$ ratios from geology at various scales. First we applied our original regression model to three additional, small watersheds within the basin to determine if the relationship can be generalized to smaller watershed scales. Next, we created a second regression model that includes $^{87}Sr/^{86}Sr$ values for these three additional watersheds to determine if prediction accuracy can be improved. We then quantified the effects of watershed scale and heterogeneity on the accuracy of regression outputs using the percentage area of rock types within basin watersheds and the Shannon index of diversity and evenness.

Finally, the relationship between geology and $^{87}Sr/^{86}Sr$ chemistry offers the possibility that researchers could quantify whether a study area is amendable to isotopic research before valuable time and resources are expended in sample analysis. We tested our ability to use geologic maps directly, without water sampling, to determine whether watersheds are distinguishable, and thus amendable to isotopic study. We used watershed geologic data as the independent variable in a linear discriminate function with major watersheds as the dependent variable. Our ability to distinguish watersheds using this method was then compared with the results based on water sampling. Finally, we analyzed the geologic differences required for two watersheds to be distinguishable using logistic regression on the pairwise comparisons of the major Snake River watersheds.

All statistical analyses were conducted in R statistical package (versions 2.10.1 and 2.15.1, http://www.r-project.org/).

2.1. Study site

The Snake River, the largest tributary to the Columbia River, drains an area of 280,000 km^2 encompassing six states (Fig. 1). Fall Chinook salmon, which spawn in the lower reaches of the major tributaries in the basin, are listed as endangered under the Endangered Species Act (April 22 1992, Federal Register, Vol 57, No 78, p 14653). Fall Chinook salmon in the Snake River inhabit a river system that has been significantly altered by hydropower construction, blocking upstream access to the majority of fall Chinook salmon spawning grounds and impounding a large portion of the downstream habitat behind eight hydropower dams.

The Snake River tributaries can be grouped broadly by geology (Fig. 1). The Clearwater and Salmon Rivers flow over felsic rocks of the Idaho batholith, with the Clearwater being influenced most heavily by the older metamorphic rock (Foster and Fanning, 1997). The Tucannon, Grande Ronde and Imnaha Rivers flow primarily over the Columbia River Basalts (Hooper et al., 2007), with the Grande Ronde and Imnaha Rivers being influenced in their headwaters by the more diverse Wallowa terrane (Hales et al., 2005). The upper Snake River begins in the geologically more diverse and older Teton Range (Love et al., 1978), and the basalt and rhyolites of the Snake River Plain (Leeman, 1982). The unique geologic conditions through which each group of rivers flows lead to detectable differences in geochemical fingerprints between rivers in the Columbia River Basin.

Geochemical variation among basin tributaries has allowed previous classification of salmon spawning and rearing areas based upon geochemical signature (Hegg et al., 2013). Hegg et al. (2013) classified the main tributaries and Upper and Lower Snake River into four groups based upon $^{87}Sr/^{86}Sr$ ratio in stream water using a linear discriminate function. Otoliths from returning adult fall Chinook salmon were then analyzed and the $^{87}Sr/^{86}Sr$ signatures from their natal, rearing and overwintering stages were recovered using laser ablation inductively

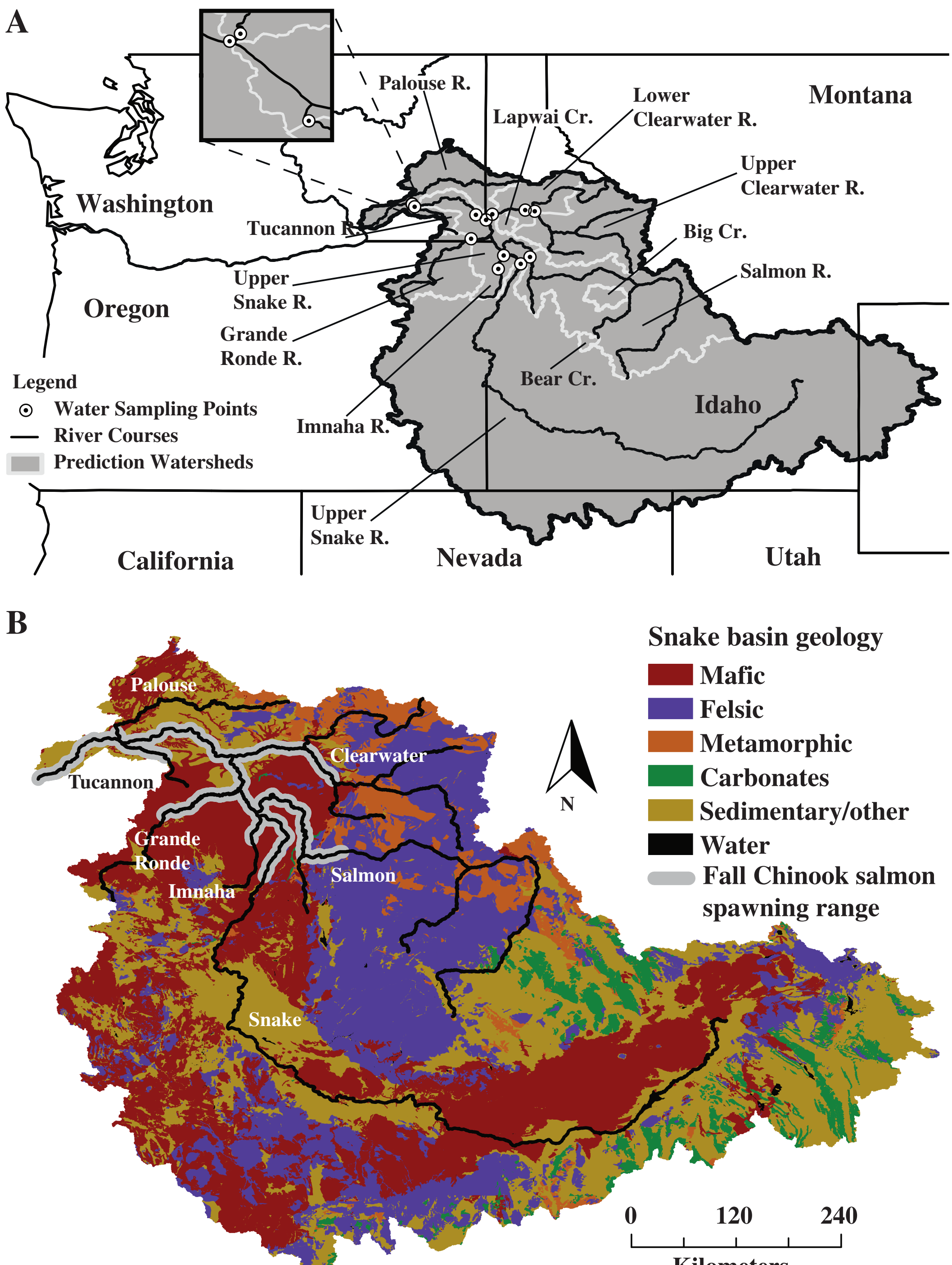

Fig. 1. The location (A) of the Snake River basin and the watershed boundaries and water sample points used to predict $^{87}Sr/^{86}Sr$ ratios are shown. Watersheds are nested; downstream watersheds include all upstream watersheds. Lithology of the Snake River watershed (B) shows rock type categories with strong impacts on $^{87}Sr/^{86}Sr$ ratio based primarily on protolithic composition (Ludington et al., 2005; Stoeser et al., 2006).

coupled plasma mass spectrometry. The location of each fish at these life history points was then determined by classifying the $^{87}Sr/^{86}Sr$ signatures using the linear discriminate function developed from water sampling across major basins.

In the research presented here, we aimed to determine the location of these fish using geologic predictions of streamwater $^{87}Sr/^{86}Sr$ ratio developed from a regression of known $^{87}Sr/^{86}Sr$ samples and geologic data, then examine whether the spatial scale or resolution of fish location could be increased using prediction. Therefore, we used the stream water $^{87}Sr/^{86}Sr$ signatures and the juvenile rearing phase of the above otolith dataset to test our ability to determine fish origin using predictions of $^{87}Sr/^{86}Sr$ values from bedrock geology.

2.2. Quantifying bedrock geology

Our geological analyses were based upon current bedrock geologic maps from the Preliminary Integrated Geologic Map Database of the United States (Ludington et al., 2005). These maps detail the bedrock geology of the Snake River basin at 1:500,000 scale with consistent lithology across the region. The primary rock type within each map polygon is recorded in the attribute table of the map layer according to LithClass 6.1 standard (http://www.nadm-geo.org).

While quantifying geologic variability within our study area we focused our analyses on percent abundance of rock types within a basin rather than rock age. Rock age has an effect on $^{87}Sr/^{86}Sr$ due to the evolution of radiogenic ^{87}Sr from ^{87}Rb over time (half life of 48.8 billion years); however, quantifying this relationship is complicated for two reasons. First, the covariation of rock age with rock type within the Snake River basin would not allow us to distinguish causality. For example, the Idaho Batholith, a granitic structure that would be expected to have high $^{87}Sr/^{86}Sr$, is also generally older and associated with extremely old, high $^{87}Sr/^{86}Sr$, metasedimentary deposits, making it difficult to determine the relative contribution of age and rock type in the $^{87}Sr/^{86}Sr$ values. Conversely, the Columbia River basalts are relatively young, but would also be expected to have low $^{87}Sr/^{86}Sr$ based upon their mafic composition. Secondly, acquiring reliable and comparable geologic ages for watersheds across the large Snake River basin proved challenging. There can be large variation in the range of ages reported for a given rock type polygon and rock age varies in its precision between different map units. The addition of age did not significantly improve our predictive ability, likely due to the factors mentioned above, and therefore we only used geologic type in this analysis.

Our aim in reclassifying rock types was to capture the geologic variation relevant to $^{87}Sr/^{86}Sr$ differences in stream water. Our rock type classification was primarily based upon distinguishing between mafic and felsic rock types since these broad rock types typically display different strontium isotopic chemistry based upon the composition of their magma source (Faure and Mensing, 2004). Thus, all igneous rocks were classified by either mafic or felsic rock type. We distinguished all non-igneous rocks by their protolithic rock type when the protolith was obvious from the map entry. Many non-igneous rock types have no obvious protolithic composition. When no obvious protolith could be determined the rock types were then classified into categories of metamorphic, carbonate, or sedimentary/other.

The potentially high rates of weathering in carbonate rocks can have large impacts on $^{87}Sr/^{86}Sr$ ratios within a watershed, so carbonate rocks were given their own classification (Blum et al., 1998). We designated a metamorphic rock category based on prior knowledge that high $^{87}Sr/^{86}Sr$ values might be present in very old metamorphic systems associated with the Idaho batholith (Martignole et al., 2010; Jansen, 2011). The sedimentary/other classification included rocks and unconsolidated sedimentary deposits of indeterminate origin as well as chemical and biogenic deposits other than carbonates. The details of rock reclassification are listed in Table 2 of the online Appendix.

2.3. Surface area calculation

Surface area may be important when calculating the relative contributions of geologic types. Differential weathering and the propensity for more resistant rock types to form vertical faces may bias the flat map area toward the least resistant rock types. We used 3-dimensional (3D) surface area alongside the conventional 2-dimensional (2D) map area to determine whether 3D area might be a better predictor of $^{87}Sr/^{86}Sr$.

Three-dimensional surface area was calculated for the entire Snake River basin using 90 meter elevation rasters available from the National Elevation Dataset (Gesch et al., 2009) and the DEM surface tools package from Jenness Enterprises (Jenness, 2012). The total 2D and 3D surface area of each rock type within each sample watershed was then calculated using the Zonal Statistics tool available in the Spatial Analyst toolbox in ArcMap. Thus, two geologic datasets were produced, one recording the flat 2D area of each rock type within the basin and another which recorded the calculated 3D surface area.

The watershed above each water sample point was delineated using the ArcHydro extension for ArcMap 9.3 (ESRI). In ArcMap, the intersection between the watershed boundaries and the geologic map layer was used to calculate the 2D and 3D area of each rock type within the watershed above each sample point. The percent area of each rock type for both 2D and 3D maps was then calculated from the attribute table of the intersected map.

2.4. Model selection and prediction of $^{87}Sr/^{86}Sr$ from geology

Multiple linear regression was used to develop a relationship between $^{87}Sr/^{86}Sr$ watershed geology within the spawning area of Snake River Fall Chinook salmon. To develop this regression, percent geologic area was the independent variable, while the $^{87}Sr/^{86}Sr$ values from 13 watersheds in the Snake River from Hegg et al. (2013) were used as the dependent variable. Percent rock area followed an exponential relationship with $^{87}Sr/^{86}Sr$ and was transformed using $\log(x + 1)$ to meet the assumption of linearity and account for real zero values within the data (Bartlett, 1947).

The most likely candidate models were compared (Table 3 online Appendix) using AICc, a version of Akaike's Information Criterion modified for small datasets (Burnham and Anderson, 2002). This statistical technique selects the model that best explains variation in the data while rewarding parsimony by penalizing over-parameterization.

Candidate models were constructed using rock types that were well represented in the basin, and rock types that were expected to have a significant influence on dissolved $^{87}Sr/^{86}Sr$ values within the study area. Based upon the large areas of mafic and felsic rock within the basin these rock types were considered good candidate variables. Similarly, the age and high $^{87}Sr/^{86}Sr$ composition of metamorphic rock in the study area indicated that it might be an important variable. All other rock types were considered to have a representation that was either of minor significance or too variable in composition to be effective predictors.

Our ultimate aim was to re-classify the fish from (Hegg et al., 2013) using a linear discriminate function and training set based on $^{87}Sr/^{86}Sr$ predictions from bedrock geology. To do this, we digitized prediction points at 10 river-kilometer (10-rkm) intervals (Fig. 3) within the spawning area of Fall Chinook based on spawning site surveys (Garcia et al., 2008). The watershed upstream of each prediction point was then delineated using ArcHydro and the percent area of each rock type was calculated. The $^{87}Sr/^{86}Sr$ value for each point was predicted by applying our regression equation to the geologic data at each point. Prediction points were then grouped according to the four river groupings (Table 1) from Hegg et al. (2013), and a linear discriminate function was created using these points as training sets.

2.5. Rearing origins classification from otoliths

We used the regression relationship developed in the previous section to test whether geologic predictions can be used to extend ecological studies using $^{87}Sr/^{86}Sr$ as a tracer. We used results from our regression to classify 127 salmon otoliths to rearing location based on the $^{87}Sr/^{86}Sr$ signature of their otoliths. We then compared these classifications to prior classifications from Hegg et al. (2013) who used stream water $^{87}Sr/^{86}Sr$ samples as a training set. Fish were classified to rearing location using the linear discriminate function we developed previously using geologic predictions as the training set. We then calculated the Kappa statistic (Fleiss et al., 2004) to compare the classification accuracy using geologic prediction to those of Hegg et al. (2013).

Hegg et al. (2013) estimated an 86% classification accuracy based on a single misclassification of six known-origin fish, with a cross validation error rate of 0% for the original training set. The regression equation used to create geologic predictions is based on the $^{87}Sr/^{86}Sr$ values from Hegg et al. (2013) and is thus not completely independent. Therefore, we would expect that any classification error when comparing

Table 1
Comparison of classification accuracy to classify fish to their juvenile rearing location based upon $^{87}Sr/^{86}Sr$ signatures in their otoliths. Linear discriminate functions were developed using training sets of $^{87}Sr/^{86}Sr$ ratios predicted from bedrock geology using the regression equation in Section 2.4 (rows) and from water samples (columns) collected by Hegg et al. (2013).

		Classification using water samples (Hegg et al., 2013)				
		Tucannon, Grande Ronde, Imnaha Rivers	Clearwater River	Lower Snake River	Upper Snake River	User accuracy
Classification using geologic regression	Tucannon, Grande Ronde, Imnaha Rivers	1	0	0	0	100%
	Clearwater River	0	37	1	0	97%
	Lower Snake River	0	3	83	0	97%
	Upper Snake River	0	0	0	2	100%
Producer accuracy		100%	93%	99%	100%	

our fish geologic regression based classifications to those of Hegg et al. is due to the error in predicting $^{87}Sr/^{86}Sr$ from geology.

2.6. Effects of scale and heterogeneity

To test the effect of watershed scale on our ability to predict $^{87}Sr/^{86}Sr$ ratios, we applied our regression model from Section 2.4 to three smaller basins within the Snake River, each with varying geologic makeup (Table 1, Online Appendix). These watersheds were chosen as a test of scale due to their smaller size. They were not included in the original geologic regression because they are outside the spawning range of Snake River Fall Chinook salmon. They were also chosen due to the existence of $^{87}Sr/^{86}Sr$ values for their tributaries, allowing additional analysis of the relationship of $^{87}Sr/^{86}Sr$ to geology at these smaller scales.

GPS locations and $^{87}Sr/^{86}Sr$ values for 19 sites within the Big Creek watershed, a tributary of the Middle Fork Salmon River, were obtained from Hamann and Kennedy (2012) (Fig. 1, Online Appendix). Six $^{87}Sr/^{86}Sr$ values and GPS locations were collected from Lapwai Creek, a tributary to the Clearwater River (Fig. 2, Online Appendix). Twelve $^{87}Sr/^{86}Sr$ water samples and GPS coordinates were also used from Bear Valley Creek, in the headwaters of the Middle Fork Salmon River, as part of a prior feasibility study in cooperation with the US Forest Service (Kennedy, unpublished data) (Fig. 3, Online Appendix). All $^{87}Sr/^{86}Sr$ values were determined using Thermal Ionization Mass Spectrometry (TIMS) except Lapwai Creek, which was analyzed using Multi-Collector Inductively Coupled Plasma Mass spectrometry (MC-ICPMS).

The geologic makeup of these additional watersheds was determined using the same techniques as for the larger Snake River basin in the preceding sections. Then, $^{87}Sr/^{86}Sr$ ratios were predicted using the regression model created in Section 2.4 to test the extent to which this regression was scale independent. We then fit a second regression model to the combined $^{87}Sr/^{86}Sr$ data for all water samples (Snake River, Lapwai Creek, Bear Valley Creek and Big Creek) to test whether a predictive model could be created which encompassed a larger range of watershed scales. Candidate models using the combined data were constructed using the same independent variable combinations of 2D mafic, felsic and metamorphic rock and selected using AICc.

To analyze how the varying representation rock types within watersheds affected our ability to predict $^{87}Sr/^{86}Sr$ ratios, we calculated the Shannon index of diversity for rock types within each sampled watershed (Shannon and Weaver, 1949). In this case the Shannon diversity index (H') is used to describe the variability of rock types present within a watershed, in contrast to its more familiar application to biodiversity.

$$H' = -\sum_{i=1}^{S}(p_i \ln p_i) \quad (1)$$

H' takes into account the relative abundance (Pi) of an individual rock type and the number of rock types (S) to calculate the relative evenness and diversity of rock types within a basin. The metric varies between 0 and $\ln(S)$ with low values indicating low diversity and uneven representation of rock types.

2.7. Exploring a priori prediction from geology

We tested the ability of geology alone to be used as an *a priori* classifier of location, without first predicting $^{87}Sr/^{86}Sr$ values using linear regression. This was done with the intent of providing a quantitative method for determining whether $^{87}Sr/^{86}Sr$ ratio may be useful as a tracer, before $^{87}Sr/^{86}Sr$ values are known within the system or before a research project is undertaken. We used the percent area of mafic and metamorphic rock types from the watershed upstream of each 10-rkm point predictions as the explanatory variable to create a linear discriminate function. We used the four chemically distinct river groups from Hegg et al. (2013) as the classification variable in this discriminate function. In this way we were able to test the ability of geologic data alone to determine which watersheds are likely to be distinguishable within a basin. We then calculated the cross-validation error rate to determine whether geology alone could distinguish rivers within the basin.

We examined the change in $^{87}Sr/^{86}Sr$ ratio for a given amount of change in geology within a watershed, and the probability that two watersheds can be distinguished by $^{87}Sr/^{86}Sr$ ratio given the difference in their geologic makeup. To do this we first calculated the pairwise differences in $^{87}Sr/^{86}Sr$ values, geologic diversity, mafic, metamorphic and felsic rock for all combinations of the watersheds used in the original 13 watersheds from Hegg et al. (2013). Then the difference in $^{87}Sr/^{86}Sr$ value was regressed against each geologic variable to understand the change in $^{87}Sr/^{86}Sr$ value for a given change in $^{87}Sr/^{86}Sr$. Finally, each pairwise watershed comparison was assigned as distinguishable or indistinguishable based on whether the watersheds were part of the same or distinguishable river groups in Hegg et al. (2013). We then used logistic regression to determine the probability that two watersheds are distinguishable given their difference in each geologic variable. Error was estimated for both linear and logistic regression as a 95% confidence interval using the standard error output of the regression.

3. Results

3.1. Model selection for prediction of $^{87}Sr/^{86}Sr$ from geology

Model fit for multiple linear regression of the Snake River water samples and bedrock geology was assessed using AICc weights (Table 3, online appendix). All models were significant ($p > 0.05$, $\alpha = 0.05$) and accounted for greater than 70% of the variation in the data. Models containing predictors calculated using 3D area outperformed the same models using 2D area. The model with the highest AICc weight was constructed using 3D area,

$$^{87}Sr/^{86}Sr = 0.0710050 - 0.005571 \cdot \log(\%Mafic + 1) + 0.015923 \cdot \log(\%Metamorphic + 1) + \varepsilon \quad (2)$$

followed closely by the same model,

$$^{87}Sr/^{86}Sr = 0.0710131 - 0.005723 \cdot \log(\%Mafic + 1) + 0.015871 \cdot \log(\%Metamorphic + 1) + \varepsilon \quad (3)$$

using 2D area. Both of the top models explained 97% of the variation in the data. While the 3D models had higher AICc scores, the difference in prediction accuracy between 2D and 3D was less than 1%. Since our goal was to create a relationship between $^{87}Sr/^{86}Sr$ and geology which can be easily utilized by researchers, this slight increase in accuracy did not justify the extra calculations involved in determining 3D area. Therefore, we used the 2D model for subsequent analyses. The results of geologic reclassification and watershed delineation are described in Table 1 of the online Appendix.

3.2. Rearing location classification from otoliths

Developing a linear discriminate function using $^{87}Sr/^{86}Sr$ calculated at 10-rkm intervals using the geologic regression from Section 2.4 resulted in a 3% classification error rate (3 misclassified out of 93 total prediction points) using leave-one-out cross validation. This same discriminate function, when used to classify fish, classified 97% (124 of 127) of fish to the same rearing location as Hegg et al. (2013) with a Cohen's Kappa of 0.93 (st. error = 0.03, C.I. = 0.86–1) indicating high agreement between methods when accounting for random error (Table 1, Fig. 2). Proportions of fish classified to each source group are not significantly different between methods (Monte Carlo Chi-Square, $\alpha = 0.05$) indicating that predictions of $^{87}Sr/^{86}Sr$ are capable of predicting fall Chinook natal origins.

The three misclassified fish had a signature intermediate between the Clearwater and Lower Snake River, similar to the single known-origin juvenile misclassified in Hegg et al. (2013). This known-origin juvenile originated in the Clearwater, but was captured in the Lower Snake River during the rearing period. Hegg et al. (2013) speculated that this misclassification may have been due to incomplete equilibration of the otolith signature to the Lower Snake environment, potentially due to the rate at which juveniles outmigrate from their natal streams.

3.3. Effects of scale and heterogeneity

Geologic diversity, as a function of both the representation and evenness of the lithology within a watershed, was greatest for the Snake River watershed. As expected, the largest watersheds displayed the highest overall diversity of rock types and geologic diversity decreased with watershed size. The three small watersheds used to test the effects of scale had the lowest geologic diversity (Fig. 3A).

Error increased significantly when predicting $^{87}Sr/^{86}Sr$ within the three smallest watersheds using the regression developed in Section 2.4 relating $^{87}Sr/^{86}Sr$ from water samples to watershed geology. This is expected when extrapolating to finer scales than the data originally used to create the regression. While residuals for the Snake River watershed samples were quite small and centered on zero (mean = $6.9 \times 10^{8} \pm 0.000457$ 1-st. dev.), the combined residuals for the three small watersheds were much higher (Mean = -0.001439 ± 0.002259 1-st. dev.) and tended to be positively skewed, indicating that the relationship of $^{87}Sr/^{86}Sr$ to geologic makeup does not follow the same relationship at smaller scales. Of the small watersheds, Lapwai Creek best fit the model, followed by Big Creek and Bear Valley Creek.

When dissolved $^{87}Sr/^{86}Sr$ samples and geologic results from the Snake River, Big Creek, Lapwai Creek and Bear Valley Creek were combined to create a comprehensive linear regression, the model with the highest AICc weight included mafic and felsic rock as independent variables (Table 4, online Appendix). The model was significant ($p < 0.0001$, $\alpha = 0.05$), however variance explained by the model ($R^2 = 0.64$) was less than the original regression model.

3.4. Exploring a priori prediction from geology

The discriminate function developed using percent area of mafic and metamorphic geology as explanatory variables, and river groups as the dependent variable, resulted in a 3% error rate using leave-one-out cross validation. This error rate was identical to the discriminate function from Section 2.4 which was based upon the regression relationship between $^{87}Sr/^{86}Sr$ and watershed geology.

Analysis of pairwise differences between watersheds showed that increasing differences in watershed geology could be used to determine whether two watersheds were likely to be distinguishable. Regression of the difference in $^{87}Sr/^{86}Sr$ for a given difference in watershed geology showed a significant positive relationship between $^{87}Sr/^{86}Sr$ and the difference in mafic, felsic, and metamorphic geology between watersheds (Fig. 4A). Geologic diversity, as measured by Shannon diversity, also showed a significant positive relationship (Fig. 4B).

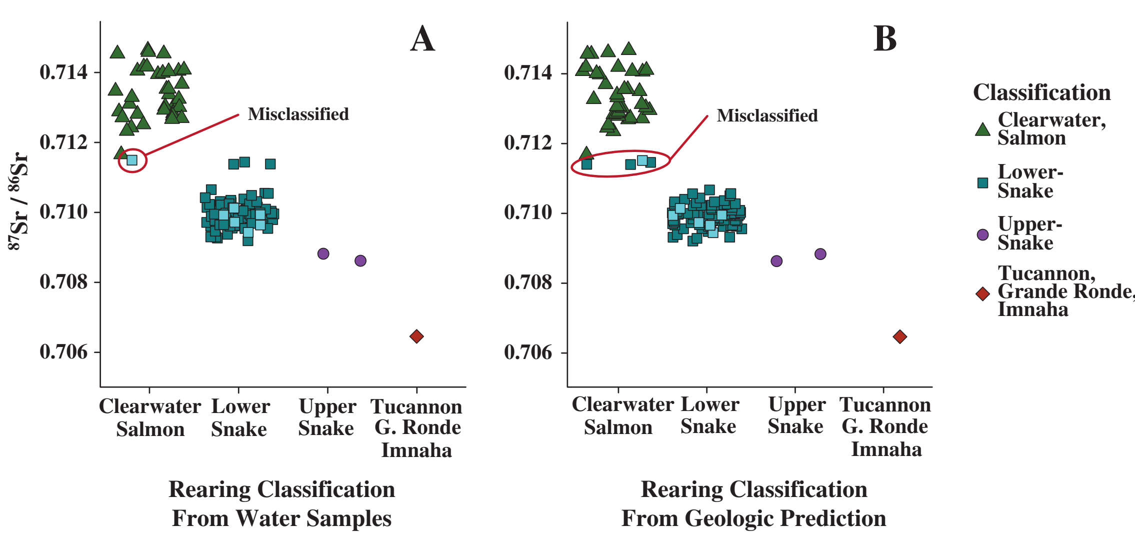

Fig. 2. Classification of adult fish to their juvenile rearing location based on $^{87}Sr/^{86}Sr$ signatures in their otoliths is shown. Classification using a linear discriminate function with water samples as the training set (A) from Hegg et al. (2013) resulted in one misclassified fish, a juvenile of known origin. Classification using a linear discriminate function based on $^{87}Sr/^{86}Sr$ ratios calculated from geology using the regression equation in Section 2.4 (B) misclassified four fish to the Clearwater group, including the fish originally misclassified in Hegg et al. (2013). Points are coded by color and shape according to statistical classification to river groups. Misclassified fish appear as a different color and shape from the classification column. Lighter colored points indicate juvenile fish of known origin. Points are jittered on the x-axis to avoid overplotting. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

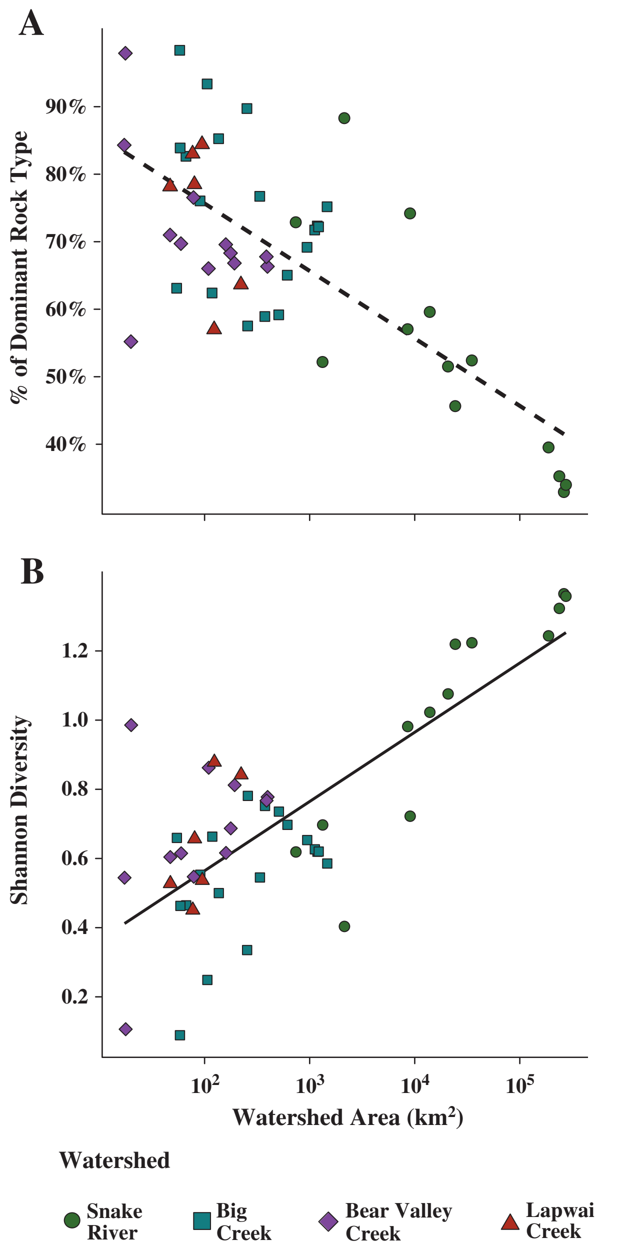

Fig. 3. (A) Geologic diversity increases with watershed scale. (B) The percentage area of the dominant rock type within a watershed decreases with watershed scale. These relationships illustrate that individual rock types begin to dominate as scale decreases, making the unique $^{87}Sr/^{86}Sr$ ratio of a given geologic formation more important at smaller scales. Dotted lines are fitted linear models to indicate the direction of the trend.

Logistic regression of the pairwise differences between watersheds showed a significant relationship between difference in watershed geology and the probability that two watersheds were distinguishable using $^{87}Sr/^{86}Sr$ (Fig. 5A). Geologic diversity also showed a significant relationship with the probability that watersheds are distinguishable (Fig. 5B). Results from the pairwise comparisons of watersheds are shown in Table 2.

4. Discussion

Naturally occurring chemical and isotopic tracers are proving to be useful and powerful methods for studying ecological questions at multiple scales (Harrington et al., 1998; Hobson, 1999; Kennedy et al., 2000; Hamann and Kennedy, 2012). Strontium isotope ratios can provide a powerful tracer of animal movement at varying scales, but baseline isoscapes are not well developed, hindering its widespread use (Hobson et al., 2010). Isoscapes for other isotope systems such as hydrogen and oxygen, which are based on large scale precipitation trends, are well developed but useful only at regional and continental scales (Bowen, 2010). Because $^{87}Sr/^{86}Sr$ can be used to track animal movement at local, regional and continental scales, $^{87}Sr/^{86}Sr$ isoscapes can be used link ecological processes across scales, a major challenge of traditional ecological studies (Hobbs, 2003). Much work is still needed to create a generalizable model of $^{87}Sr/^{86}Sr$ variation that accounts for a majority of $^{87}Sr/^{86}Sr$ variation across a broad range of geologies and scales. Our method for classifying bedrock geology by mafic or felsic protolith may help to standardize future models by providing a repeatable method that accounts for the major geologic drivers of $^{87}Sr/^{86}Sr$ variation across geologic settings.

This study shows that the relationship between $^{87}Sr/^{86}Sr$ and bedrock geology can be used to accurately reconstruct the location of aquatic organisms and extend the resolution of strontium isotopic studies beyond baseline water sampling points. This work also provides a relatively simple method by which investigators can determine *a priori* the feasibility of $^{87}Sr/^{86}Sr$ ratio as an investigative tool within a given population or watershed. By creating a linear discriminate function with the important reaches as the grouping variable and the mafic and felsic geology as the explanatory variables, the cross validation error rate can be used to give an indication of how well $^{87}Sr/^{86}Sr$ might distinguish between important reaches. Thus, it is possible to quantify the degree to which unsampled watersheds are likely to be isotopically distinct using geology alone. Further, analysis of the differences between watersheds provides relationships between geology and $^{87}Sr/^{86}Sr$, which may be useful to parameterize future predictive models of $^{87}Sr/^{86}Sr$ variation across the landscape.

4.1. Effects of scale and heterogeneity

The regression model between geologic and strontium ratio was constructed with data from a regional watershed (Snake River Basin) and performed well at that scale. However, our results indicate that the ability to predict $^{87}Sr/^{86}Sr$ from bedrock geology decreases when extrapolated to watersheds below 1000 km^2. Two factors may play a role in this loss of predictive ability. Further, creating a second regression model incorporating $^{87}Sr/^{86}Sr$ water samples from these smaller watersheds did not improve the predictive ability at smaller scales.

One factor may be that rock type classifications are broad, and can potentially obscure large underlying variation in signature. Any generalizable model predicting $^{87}Sr/^{86}Sr$ from bedrock must create broad classifications of rock types, effectively forcing rocks of variable, but similar, $^{87}Sr/^{86}Sr$ isotope chemistry to be modeled as a unit. This variation in $^{87}Sr/^{86}Sr$ values within a rock type classification can be significant, particularly for felsic rocks whose geochemical makeup, age and origin can lead to large variations in $^{87}Sr/^{86}Sr$ isotope signature (Faure and Mensing, 2004).

Second, as the size of watersheds decreases, they are increasingly dominated by single rock units rather than an average of upstream inputs (Fig. 3A), exposing the variation in $^{87}Sr/^{86}Sr$ within the felsic rock type classification. At coarse scales the model can make accurate predictions based upon broad rock types because each river is an average of the diverse signatures of the upstream watershed. Smaller watersheds however (Fig. 6A), and typically dominated by a single rock type (Fig. 6B), and therefore prediction accuracy decreases. Further, the more a watershed is dominated by felsic rock the lower the prediction accuracy of the model (Fig. 6C). This is expected since individual felsic rock units should vary widely from the mean $^{87}Sr/^{86}Sr$ of the basin based on their age and chemical makeup. Thus, as scale decreases, local variations in $^{87}Sr/^{86}Sr$ values become increasingly important for accurate prediction, and rock types containing large

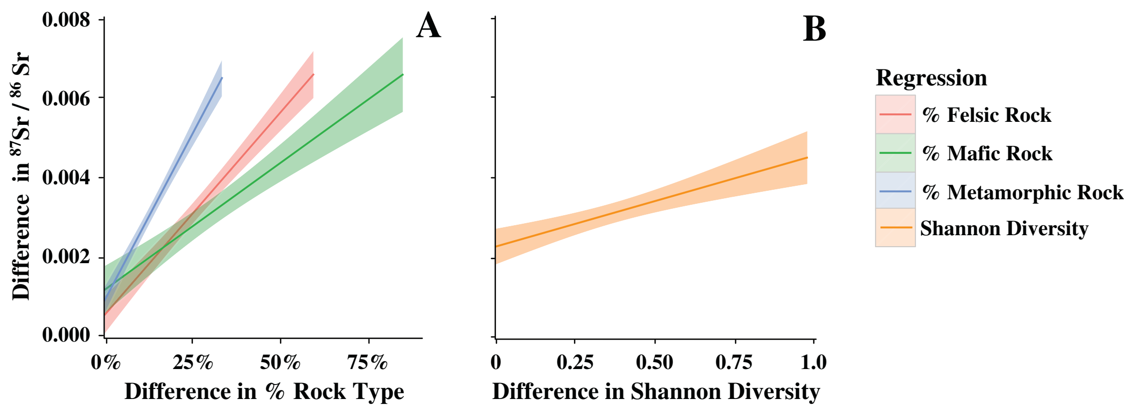

Fig. 4. The pairwise difference in $^{87}Sr/^{86}Sr$ between watersheds of the Snake River varies predictably with the difference in geologic makeup. The absolute difference in $^{87}Sr/^{86}Sr$ ratio between two watersheds shows a positive relationship with the difference in mafic, felsic and metamorphic makeup of the watersheds (A). The absolute difference in $^{87}Sr/^{86}Sr$ ratio between watersheds also follows a positive relationship with the absolute difference in geologic diversity as measured by Shannon diversity (B). Shaded area is the 95% confidence interval around the fitted line.

variation in $^{87}Sr/^{86}Sr$ signatures begin to be particularly poorly predicted. Therefore, we would expect that generalized models would perform best at the largest scales, where stream water $^{87}Sr/^{86}Sr$ signatures are an average of many rock units throughout a basin and effectively integrate the overall variation within each rock type classification. It is possible, however, that at smaller scales the difference in a given rock type could provide an indication that watersheds are distinguishable, even when the absolute $^{87}Sr/^{86}Sr$ cannot be predicted. Results from our analysis of pairwise differences between watersheds give an indication of how this could be determined.

The scale and geologic makeup at which predictions of $^{87}Sr/^{86}Sr$ ratios can be made from bedrock will be different for every watershed. Our study indicates, however, that in order to effectively apply predictions from bedrock geology or produce generalizable isoscape models, it is important to constrain the scale and geologic heterogeneity at which predictions are made. Measures of heterogeneity such as Shannon diversity and the percentage area of the dominant rock type are independent of scale and geologic makeup, and can be applied to any watershed. These metrics could potentially be used to quantitatively determine, based on the geologic heterogeneity of the watershed, a lower spatial threshold above which predictions are appropriate. In the case of the Snake River, with more than 55% of the watershed dominated by a single rock type and geologic Shannon diversity below 1.0 (H'), prediction accuracy begins to decrease substantially (Fig. 6). Spatially this corresponds to watersheds of 1000 km^2 or smaller. Further work is needed to understand if heterogeneity measures can be generalized across differing watersheds with differing geologies, and to develop quantitative methods for applying these metrics across watersheds.

4.2. Exploring a priori prediction from geology

One difficulty for researchers planning to use $^{87}Sr/^{86}Sr$ isotope ratios as a tracer is determining whether a study system contains enough isotopic variation between the important watersheds to provide meaningful results. Our results indicate that it is possible to use geologic variation as inputs to a linear discriminate function to determine *a priori* whether important watersheds are likely to be isotopically distinct. This provides a feasible *a priori* method that requires minimal time input or prior knowledge. The data requirements are minimal, only geology and watershed layers are needed. Using GIS, a researcher can then reclassify the geologic map, define the relevant watersheds, and intersect the layers. Calculating the percentage area of each rock type is then a simple calculation. Using the cross-validation error rate of a discriminate function to determine likely isotopic differentiation is not, however, a definitive test. It assumes that the major rock types within a study area are isotopically distinct but it is possible for rocks to be isotopically similar regardless of their rock type classification, which would confound the results. Therefore a more mechanistic understanding of the isotopic

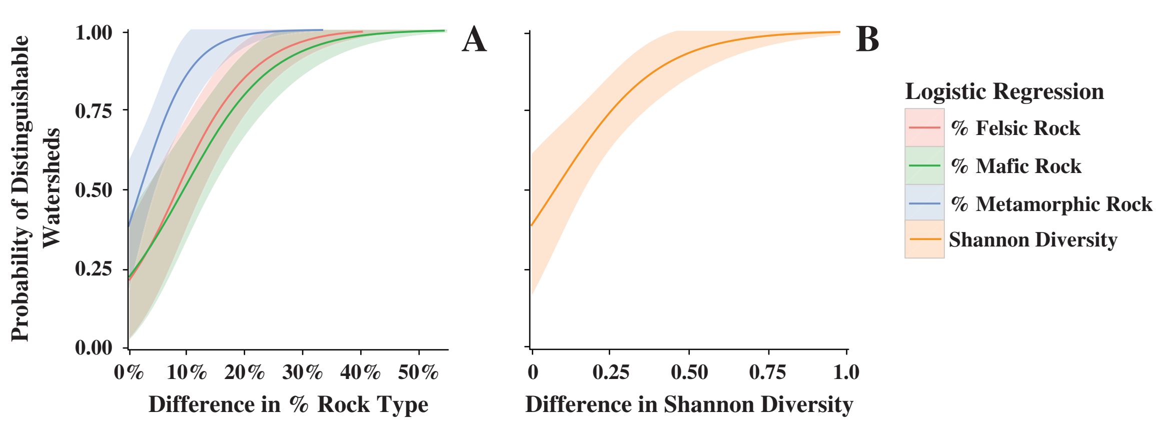

Fig. 5. As the difference in geologic makeup between two watersheds increases, the probability that they can be distinguished using $^{87}Sr/^{86}Sr$ values increases (A). Small differences in metamorphic rock in particular increase the probability that watersheds are isotopically distinct, as do mafic and felsic geology. The difference in geologic heterogeneity between two watersheds, as measured using Shannon diversity, is also a good predictor of that watersheds are isotopically distinct (B). Shaded area is the 95% confidence interval around the fitted line.

Table 2
Results of regression analysis for pairwise watershed comparisons from Hegg et al. (2013) show significant positive relationships between the difference in mafic, felsic and metamorphic geology and the difference in $^{87}Sr/^{86}Sr$ ratio using linear regression. All models and coefficients were significant ($p < 0.05$). Error is reported a ± 95% confidence interval.

Linear regression	Intercept	Coefficient
Model		
$^{87}Sr/^{86}Sr = \%\ mafic + \varepsilon$	0.0012 ± 0.0006	0.0064 ± 0.0016
$^{87}Sr/^{86}Sr = \%\ felsic + \varepsilon$	0.0006 ± 0.0005	0.0101 ± 0.0016
$^{87}Sr/^{86}Sr = \%\ metamorphic + \varepsilon$	0.0009 ± 0.0004	0.0167 ± 0.0020
$^{87}Sr/^{86}Sr = Shannon\ diversity + \varepsilon$	0.0023 ± 0.0008	0.0023 ± 0.0018
Logistic regression	**Log odds**	
Model	Intercept	Coefficient
$^{87}Sr/^{86}Sr = \%\ mafic + \varepsilon$	−1.2488 ± 1.1430	13.0494 ± 6.8689
$^{87}Sr/^{86}Sr = \%\ felsic + \varepsilon$	−1.3093 ± 1.0953	15.1571 ± 7.1456
$^{87}Sr/^{86}Sr = \%\ metamorphic + \varepsilon$	−0.4771 ± 0.8750	22.7080 ± 14.8427
$^{87}Sr/^{86}Sr = Shannon\ diversity + \varepsilon$	−0.4835 ± 0.9639	6.1581 ± 3.6998

variation within rock types is needed to provide a truly predictive *a priori* method.

Our regression results provide a more quantitative method of determining whether watersheds might be distinct. In the Snake River, watersheds with a difference of 35–40% of mafic or felsic rock type have a 95% probability of being isotopically distinct (Fig. 5A). Linear regression shows a positive relationship between the difference in percentage of rock type and the change expected in $^{87}Sr/^{86}Sr$ values, which gives a measure of the difference in $^{87}Sr/^{86}Sr$ ratios between distinguishable watersheds (Fig. 4A).

The logistic regression of metamorphic rock type provides insight into how a single, relatively rare, geology can exert an important impact on watershed differentiability. A difference of only 10% in metamorphic rock within a watershed provides an 85% probability that the watersheds are distinguishable and only 15% difference results in a 95% probability (Fig. 5A). This is an important consideration when creating future generalized models, as some rock types may exert a larger influence than their representation on the landscape would indicate.

Interestingly, our results show that a metric of geologic heterogeneity can be used to relate watershed geology to variation in $^{87}Sr/^{86}Sr$ isotopic values. A difference in Shannon diversity of 0.56 indicates a 95% probability that two watersheds are distinguishable and the linear regression shows a significant positive relationship between diversity and $^{87}Sr/^{86}Sr$ ratios (Figs. 4B and 5B). This provides additional evidence that metrics of geologic diversity may provide a means to improve $^{87}Sr/^{86}Sr$ isoscape methods.

This study shows that the relationship between $^{87}Sr/^{86}Sr$ and bedrock geology has the potential to be a useful ecological tool for the study of migration and distribution of organisms across a landscape. Though more work is needed to generalize these results outside the Snake River, they provide some insight into what might be expected in similar watersheds. Applying these methods to additional watersheds may uncover patterns in geologic heterogeneity which could place bounds on the scale and predictive ability of future models. Additionally, these analyses provide a starting point for understanding the isotopic differences we expect for a given change in geologic makeup, which could be used to parameterize future isoscape models.

Our study highlights two areas in which methods must improve for $^{87}Sr/^{86}Sr$ isoscape predictions to be generalizable. First, geologic age should be included as a variable in future models in order to explain smaller scale variation in $^{87}Sr/^{86}Sr$, especially within felsic rocks. Second, geologic heterogeneity should be explored as a method to guide future modeling efforts, particularly as a tool to determine the lower threshold of prediction accuracy. Past efforts at determining stream water $^{87}Sr/^{86}Sr$ values using geology (Barnett-Johnson et al., 2008; Bataille and Bowen, 2012; Bataille et al., 2012; Chesson et al., 2012) have focused on intrinsic characteristics of rock types. This study shows that this approach is valid, but limited by our understanding of how $^{87}Sr/^{86}Sr$ signatures vary in relation to the distribution of geologic features within watersheds and at varying scales. By applying tools of landscape ecology to understand how the spatial occurrence of geologic features affects our ability to predict $^{87}Sr/^{86}Sr$ ratios we may be able to improve predictions and better constrain the spatial limits of future models.

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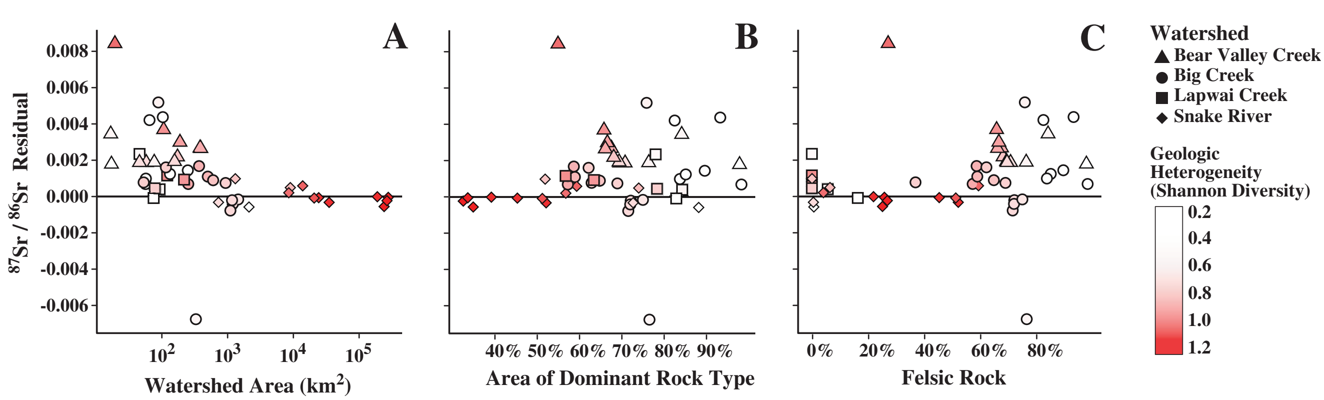

Fig. 6. The ability to predict $^{87}Sr/^{86}Sr$ ratio using bedrock lithology increases with watershed size (A). As watersheds decrease in size and are increasingly dominated by a single rock type, prediction accuracy decreases (B). As the percentage of felsic rock increases within a watershed, prediction ability decreases (C) showing that the loss of prediction ability is largely driven by felsic geology. Values for each watershed are based on water sampling and analysis using TIMS, except Lapwai creek which was analyzed using MC-ICPMS. Values for the Snake River are seasonal averages from Hegg et al. (2013), all others are single water samples.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.chemgeo.2013.10.010.

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