STABLE ISOTOPE COMPOSITION OF STREAM BIOTA:

PARTITIONING VARIABILITY AND IDENTIFYING ENVIRONMENTAL CORRELATIONS IN A WILDERNESS WATERSHED

A Thesis

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Authorization to Submit Thesis

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Abstract

Stable isotopes are used frequently in biogeochemistry and ecology to identify the use and movement of material within ecosystems . The isotopic composition of organic matter changes in predictable ways and often those changes are preserved as the elements cycle through space, time and trophic levels. Analysis of carbon, nitrogen and sulfur stable isotopes has become a common tool in aquatic stream ecology to help reveal the complex interactions and processes that occur in these dynamic systems. In this thesis, I explore patterns of stable isotope composition of periphyton and macroinvertebrates in a wilderness stream network and investigate correlations to natural environmental heterogeneity. Chapter 1 explores the spatial and temporal variability in nitrogen, carbon and sulfur stable isotope values of aquatic biota, observed trophic discrimination, and correlations with environmental landscape characteristics. I found that the nitrogen, carbon and sulfur isotopic composition of periphyton and macroinvertebrates does vary considerably in this watershed and that this variability can be partitioned and attributed to a few major factors, specifically taxon and site. Correlations with wildfire and geology appear to be more important parameters in predicting nitrogen and sulfur stable isotopes, respectively, than spawning salmon in this watershed. In Chapter 2, I utilize creative nonfiction narratives to inform non-scientific audiences on stream ecology, stable isotopes and cross-ecosystem subsidies, fostering holistic ecosystem thinking and attention to waterways as multi-directional corridors. This interdisciplinary approach to scientific research and communication effectively conveys a message to readers, increasing knowledge of stable isotope ecology and how understanding the associated variability and environmental heterogeneity promises to improve the utility of stable isotopes in measuring connectivity of disparate ecosystems

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Dedication

I would like to dedicate my master's thesis to my parents for teaching me the true measures of happiness and letting me always find my own direction. And to everyone who embraces the wonders of the natural world.

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CHAPTER 1

Partitioning sources of variability in nitrogen, carbon and sulfur stable isotopes of stream biota in an inland wilderness watershed characterized by natural wildfire history and native Chinook Salmon

Abstract

Stable isotope analysis is a common tool in aquatic ecology, yet the variability and relative influence of different environmental conditions on isotopic ratios observed in stream biota is not well resolved, especially at the regional scale. I quantify variation in nitrogen, carbon and sulfur stable isotopes in periphyton and three macroinverebrate taxa representing distinct trophic levels at 16 sites encompassing a range of salmon spawning densities, wildfire histories, and stream types in an oligotrophic wilderness watershed. For all three elements, trophic level and site accounted for most of the variability, while temporal variability across the watershed was not significant between years or between months during the summer sampling season. These results indicate the importance of developing methods to incorporate shifting baselines in isotopic mixing models, as well as identifying appropriate spatiotemporal scales for stable isotope studies in lotic systems. The relationship in nitrogen stable isotope composition between periphyton and macroinvertebrates representing higher trophic levels (grazers, collectors, predators) revealed that the basal resource, e.g. periphyton, was more closely linked to site location and less variable through time than were macroinvertebrates, but predictive relationships existed between periphyton, grazers and predators. The distinctly different nature of variability observed in collectors versus periphyton or primary consumers suggests that different target taxa may be chosen for isotopic studies based on specific research questions and the spatiotemporal scale of interest. I also investigated the relative importance of heterogeneous landscape conditions in the watershed, exploring correlations in nitrogen and sulfur stable isotopes to wildfire history, spawning salmon presence, land cover type, bedrock geology and percent cover. Predictive models attribute site differences in periphyton and macroinvertebrate δ^{15}N and δ^{34}S values to baseflow discharge (a metric for stream size), burn history of the catchment (for δ^{15}N only) and bedrock geology (for δ^{34}S only). Findings suggest that in-stream biota (periphyton and macroinvertebrates) of the Big Creek watershed, Idaho, USA do not incorporate salmon derived nutrients into their tissues. Collectively, these findings have implications for studies using stable isotopes as measures of resource use, marine-derived nitrogen incidence, and demonstrate the importance of considering watershed level factors before interpreting stable isotope data among sites.

Introduction

Stable isotope ratios of nitrogen, carbon, and increasingly, sulfur, are used in ecology to identify the use and movement of distinct energy sources within ecosystems and around the world (Hamilton et al. 1992, Michener and Schell 1994, Chamberlain et al. 1997, Hobson 1999, Post 2002, Finlay et al. 2002). They have become a common tool in aquatic and stream ecology in diverse applications including tracing energy flows (e.g. DeNiro and Epstein 1981, Peterson and Fry 1987), constructing food webs and trophic position (e.g. Cabana and Rasmussen 1996; Vander Zanden and Rasmussen 1999), developing dietary mixing models and resource use (e.g. Fry and Sherr 1989, Kline et al. 1990, Michener and Schell 1994, Phillips and Gregg 2001, Bunn et al. 2003), monitoring anthropogenic influence (e.g. Harrington et al. 1998, Huang et al. 2013, Leavitt et al. 2006) and investigating toxicology (e.g. Cabana and Rasmussen 1994, Kidd et al. 1995, Wayland and Hobson 2001, Morrissey et al. 2013, Connolly et al. 2013). Additionally, stable isotope analysis has enabled researchers to trace the movement of resource subsidies across ecosystem boundaries: from aquatic to terrestrial (Polis et al. 1997, Mellbrand et al. 2011), terrestrial to aquatic (Rounick and Winterbourn 1986, McCutchan and Lewis 2002, Rasmussen 2010), and from marine to freshwater ecosystems (Bilby et al. 1996, Naiman et al. 2002, Gende et al. 2002, Chaloner et al. 2002, Koyama et al. 2005, and many others). Many studies have now shown that marine derived nutrients—identifiable primarily by higher nitrogen isotopic ratios than in terrestrially derived nitrogen—are purveyed upstream by anadromous salmon returning to natal freshwater streams to spawn and then incorporated into multiple trophic levels in freshwater streams and riparian corridors (Kline et al. 1990, Bilby et al. 1996, Minakawa et al. 2002). These findings, among many others, substantiated the ecological significance of resources heterogeneously distributed through space and time and the utility of stable isotopes in detecting cross ecosystem subsidies and the movement of resources in general.

The reliability of stable isotope analysis has been scrutinized over the last decade, as further study has revealed a high degree of spatiotemporal variability in stable isotope ratios and trophic discrimination (Vander Zanden and Rasmussen 2001, Goedkoop et al. 2006, Bowen et al. 2010), particularly of biota in lotic systems (Finlay et al. 1999, Jardine et al. 2014). Carbon, nitrogen and sulfur stable isotopes in primary producers and consumers can naturally be quite variable across space at both large (Woodland et al. 2012, Ishikawa et al. 2012) and small scales (France 1995a, Huang et al. 2013). There can also be significant variation through time (McCutchan et al. 2003, Woodland et al. 2012, Jardine et al. 2012) and across species (Minagawa and Wada 1984, Peterson and Fry 1987, Lancaster and Waldron 2001, Post 2002).

While predictable differences in stable isotope composition of various organisms and locations is arguably exactly what makes them so useful, a number of studies have provided inconclusive evidence for the mechanisms of this variation leading to uncertainty in their interpretation or utility (Finlay et al. 1999, Hadwen et al. 2010, Duda et al. 2011, Reisinger et al. 2013). For example, elevated $\delta^{15}N$ and $\delta^{13}C$ values are commonly used as evidence for incorporation of marine derived nutrients in freshwater stream biota (Hicks et al. 2005, Chaloner et al. 2002), but changes in δ^{15}N and δ^{13}C values of periphyton may reflect shifts in growth rate, water velocity, watershed area or other abiotic factors (Macleod and Barton 1998, Harrington et al. 1998, Finlay 2001, Trudeau and Rasmussen 2003, Hobson 2010) rather than the presence or absence of salmon (Pinay et al. 2003, Duda et al. 2011).

The underlying causes and patterns of isotopic variability in stream biota are complex and difficult to detect or interpret even when additional information accompanies interpretations and conclusions. Many efforts have been made to identify the factors influencing carbon stable isotope composition of aquatic biota and results point to a variety of physical and biological processes. Watershed size (Finlay 2001), week (Hawden et al. 2010), season (Ishikawa et al. 2012), growth rates and biomass accumulation (Hill and Middleton 2006), microhabitat and water velocity (Finlay et al. 1999, Huang et al. 2013), stream productivity (Finlay 2004), flow history (Singer 2005), land use (Winemiller 2011), life stage of organism (Alp 2013), dissolved CO_2 (Finlay 2004), biome (Ishikawa et al. 2012), δ^{13}C of carbon sources and boundary layer thickness (Keeley and Sandquist 1992), light (Rounick and Winterbourn 1986, Finlay 2001), trophic fractionation (DeNiro and Epstein 1978, Finlay 2001), and microbial, fungal and detrital contamination (Hamilton et al. 2005) have all been investigated as factors influencing carbon stable isotopes in lotic biota. The majority of these studies exclusively dealt with δ^{13}C values of primary producers. Despite this literature, in a global meta-analysis on carbon isotope variability in food web and dietary mixing models studies, Ishikawa et al. (2012) concluded that variation in $\delta^{13}C$ values of freshwater autotrophs is not yet fully understood. The carbon stable isotope composition of autotrophs directly and indirectly impacts that of higher trophic levels, and thus has implications for stable isotope studies at all spatial, temporal scales and with a focus on any trophic level.

Understanding nitrogen stable isotope variability also has implications for stream ecology and other studies employing stable isotope analysis. For example, in fisheries and ecosystem management there is a widespread mentality that marine derived nutrients have major implications for salmon population viability based on studies exploring nutrient feedback cycles from spawning salmon to freshwater juveniles (Bilby et al. 1998, Wipfli et al. 2003, Holecek et al. 2009, Kohler et al. 2013, Achord et al. 2003). Others caution universal application of these methods and conclusions, asserting that the drivers of $\delta^{15}N$ patterns are less well understood than for carbon, especially outside of trophic fractionation (Woodland et al. 2012, Jardine et al. 2014). As with carbon, $\delta^{15}N$ values depend on many different biological and physical processes including nutrient enrichment (McClelland and Valiela 1998, Harrington et al. 1998, Cole et al., 2004, Leavitt et al. 2006, Kohler et al. 2012), nutrient limitation (Trudeau and Rasmussen 2003), salmon presence and abundance (Bilby et al. 1996, Verspoor 2010 et al., Holtgrieve et al. 2010), temperature (MacLoed 1998, Power et al. 2003, Friberg et al. 2009), riparian vegetation (Adams and Sterner 2000), organism life stage (Alp et al. 2013), body tissue turnover rates (Post 2002), concentration and isotopic signature of dissolved inorganic material (Owens 1987, Macloed and Barton 1998), wildfire (Spencer et al. 2003, Mihuc and Minshall 2005), light availability (Macloed and Barton 1998, Ambrose et al. 2004, Verspoor et al. 2010), source precipitation, soil and nutrient characterisrics (Heaton 1986, Evans 2001), geomorphology (Holtgrieve et al. 2010, Hladyz 2011), hydrology (MacLoed and Barton 1998, Verspoor et al. 2010, Duda et al. 2011, Huang et al. 2013), and nitrogen cycle transformations such as decomposition and denitrification (Benner et al. 1987, Currin et al. 1995, Pinay et al. 2003).

Sulfur has been utilized much less than carbon and nitrogen, primarily because it is more difficult to isolate, more expensive to analyze, and potentially more difficult to interpret (Fry et al. 2002, Connolly et al. 2004). There is no predictable or reliable discrimination in sulfur isotopes between diet and consumer as it is metabolized (Fry 1988, Hobson et al. 2010), minimizing its utility in trophic position estimates, but potentially increasing its utility in tracing movement of matter across space and through food webs (e.g. Ofukany et al. 2012). Because sulfate reduction creates strong differentiation in $\delta^{34}S$ values (Peterson and Fry 1987, Zhang et al. 1998), sulfur stable isotope ratios can depict distinct aquatic habitat conditions across space (Hesslein et al. 1991, Deegan and Garritt 1997, MacAvoy et al. 1998, Fry and Cumchal 2011). They have proven most useful in tracing nutrient flows in or near marine and estuarine systems (Peterson et al. 1986, Hesslein et al. 1991, Michener and Schell 1994, Fry et al. 2002, MacAvoy et al. 1998, MacAvoy et al. 2000, Connolly et al. 2004, Fry and Cumchal 2011, Ofukany et al. 2012) and areas subject to acid precipitation or dominated by anoxic conditions (Kaplan and Rittenberg 1964, Alewell et al. 1999). Sulfur stable isotopes are used less in freshwater stream studies, but occasionally employed to identify cross ecosystems movements (Kline et al. 2007, Wayland and Hobson 2003), in diet partitioning studies (Fry et al. 2002, Swanson et al. 2011), and have been very helpful in separating sources in food webs when C and N do not resolve questions (Connolly et al. 2004, Connolly and Schlacher2013).

The mechanisms driving changes in stable isotope ratios in lotic biota likely vary in importance and complexity in different systems. Taken together, the varied responses and mechanisms suggested by these studies and others highlight the need for further work before we fully understand controls of isotopic variability in natural biological systems, and perhaps more importantly to facilitate more appropriate use the variation in stable isotope analysis to better understand ecosystem and ecological processes.

The C, N and S isotopic composition of different organisms (and the relationships between trophic levels) has implications for what species or taxa is most appropriate to target as an isotopic baseline in food web and resource use studies. A common challenge encountered in field-based stream food web studies is identification and isolation of specific diet-consumer connections, especially in lower trophic levels, due to the ubiquity of omnivory and generalist feeding strategies (Peterson and Fry 1987, Vander Zanden and Rasmussen 1999, Anderson and Cabana 2007). End member mixing models have been adopted as a common tool to unravel these complex connections and help identify sources of organic matter ($\delta^{13}C$) and food web structure ($\delta^{15}N$) (Cabana and Rasmussen 1996, Jardine et al. 2014). However, mixing models suffer greatly from highly variable inputs, which is an unfortunately common characteristic of primary producer stable isotope data

(France 1995b, Phillips and Gregg 2003, Finlay 2004, Hadwen et al. 2010). As a result of high variability found in aquatic primary producers, the general trend is now to use primary consumers as an isotopic baseline in resource use and food web studies using stable isotopes (Cabana and Rasmussen 1998, Post 2000, McCutchan and Lewis 2002). However, there is still much discussion in the literature on best practices and interpretation of the results and the choice of target organisms may depend on the spatial scale of interest and specific research questions of the study.

As research continues into the physiological processes of trophic discrimination in stream biota we are increasing understanding of the magnitude and importance of such processes. Nevertheless, the uncertainties in this field warrant a good deal of caution when trying to interpret the data (Gende et al. 2002) and in response to others' warnings (Alp et al. 2103, Bergfur et al. 2009) I assessed fractionation rates in different taxa, specific to this study system, before trying to interpret cross-boundary trophic linkages and environmental correlations. Programs such as IsoSource or IsoConc may have applications in this realm, as might Bayesian methods, but these are beyond the scope of this project as my objectives focused on capturing patterns and correlations relevant to ecologists rather than mechanistic understanding of the food-web (Phillips and Gregg 2003). Given that the variability in both stable isotope ratios *and* trophic discrimination are known to vary between systems, I also stress the utility of this study in providing applicable methods for other researchers to investigate location specific isoscape patterns and their environmental correlations.

As an alternative to resource use mixing models, a gradient approach has recently been developed and put into practice (Bunn et al. 2013, Rasmussen 2010, Jardine et al. 2014). This is typically used to examine the reliance of a primary consumer on algal resources (Rasmussen 2010, Bunn et al. 2013, Jardine et al. 2014) but I extend it to multiple trophic levels, augmenting my investigation of trophic enrichment and observed discrimination in a natural system. This study improves understanding of isotopic variability of three elements (C, N, S) in different trophic levels through both space and time, and provides context for moving forward in the face of inherent variability.

Furthermore, relatively little is known about the *relative importance* of factors that control isotopic composition of biota in lotic systems. This is particularly true for environmental factors at the landscape scale, such as wildfires, keystone species presence, land cover type, bedrock geology, etc. Although more attention is being drawn to the relationship between stable isotope ratios and environmental heterogeneity through isotopic landscape, or isoscape, studies (Fry 2009, Bowen 2010, Bai et al. 2013) few of these have focused on carbon, nitrogen or sulfur in biological systems (but see Pardo and Nadelhoffer 2010) despite the acknowledged need (Ramsay et al. 2012, Reisinger et al. 2013). Perhaps a limited number of studies have addressed the relative importance of these landscape characteristics on stable isotopes in stream life because it can be difficult to develop a study at a scale that encompasses an appropriate amount of environmental heterogeneity. Understanding which factors are most influential at different spatial and temporal scales for a range of trophic levels is critical because of its ability to inform and improve experimental design in future studies and augment conclusions drawn from stable isotope data itself (Davis et al. 2013). In the present study, I apply the knowledge from other studies in a comprehensive, field-based study of carbon, nitrogen and sulfur stable isotope composition and variability of primary producers and consumers in a large wilderness watershed characterized by a mosaic of environmental conditions. In particular, nitrogen and sulfur were of interest to the study because they have been evaluated less than carbon at this scale and because these elements are stronger tracers of MDNs (Kline et al. 2007).

The overall goal of this study is to better understand drivers of spatiotemporal and taxonomic variability in stable isotope ratios of carbon, nitrogen and sulfur of stream biota across an oligotrophic watershed characterized by natural wildfire regime and wild anadromous salmon populations. Specifically, I aimed 1) to determine whether time, space or taxa explains more of the variability in observed isotopic ratios for each element and if the main effects are consistent across trophic levels, 2) to investigate the relationship between δ^{15}N values of basal resource and macroinvertebrates at higher trophic levels, and 3) to evaluate the relative influence of various environmental conditions on the consistency of the isotopic composition of stream taxa, with the specific aim to determine if marine derived nutrients from spawning salmon are being incorporated into the food web locally or regionally considering the coupled low salmon spawning densities and oligotrophic nature of the system. Collectively, these three objectives carried out across a network of comparative and hierarchically nested sites, allowed me to ask the extant to which values of periphyton $\delta^{15}N$ predict that in higher trophic levels across a drainage basin and how trophic fractionation rates for this relatively pristine, inland headwater system. Understanding the relative effects of trophic level, space, time and environmental conditions on isotopic variability will help improve interpretation of stable isotope-based studies conducted in similar systems and inform experimental design of future studies to streamline field sampling and laboratory isotopic analyses depending on the taxa or scale of interest.

Methods

Study Area

This study was conducted in the Big Creek watershed (1543 km^2, mean elevation 2103m), which is located in a remote region of central Idaho approximately 80 km east of McCall, Idaho, USA, and lies almost entirely within the boundaries of the Frank Church-River of No Return (FC-RONR) Wilderness area (Figure 1). Big Creek is a tributary to the Middle Fork of the Salmon River, a designated National Wild and Scenic River. The topography is complex; hillslopes average 45–70% and are dominated by poorly developed, shallow soils (Minshall et al. 2001). The geology of the area is dominated by units from the Eocene and middle to Late Proterozoic, with rhyolite (37%), granite (16%) and syenite (11%) as the predominant major rock types (Lewis et al. 2012). The climate is semiarid (mean annual precipitation: 70 cm) and is historically snow-dominated (USGS 2007). Three types of land cover dominate the watershed: evergreen forest (57%), shrub/scrub (23.3%) and grassland/herbaceous cover (18.9%) (J. Fry 2011). Evergreen forests in upper Big Creek are predominantly Douglas-fir *Pseudotsuga menziesii* and lodgepole pine *Pinus contorta*, while lower Big Creek has more ponderosa pine *P. ponderosa* and sagebrush *Artemisia spp* and is generally less forested (Holecek et al. 2009). Riparian vegetation adjacent to study sites is predominantly alder, water birch, red-osier dogwood and a variety of grasses, shrubs and forbs (willow, rose, horsetail, etc). Wildfire is an active ecological force in this wilderness area, and large portions of the Big Creek watershed have burned with varying severity in six of the last thirteen years (Figure 2) (Morgan et al. 2008). Additional relevant ecological information on the FC-RONR wilderness area can be found in Thurow (2000) and Minshall (1981).

The Big Creek stream network contains a diverse community of fish including many salmonids: Chinook salmon *Oncorhynchus tshawytscha,* bull trout *Salvelinus confluentus*, brook trout *S. fontinalis*, westslope cutthroat trout *O. clarkii lewisi*, steelhead *O. mykiss*, and mountain whitefish *Prosopium williamsoni* (Holecek et al. 2009). The local population of Chinook salmon is part of the Snake River spring–summer Chinook Salmon Evolutionarily Significant Unit, considered threatened under the Endangered Species Act as of 1992 (NMFS 1992). It is one of few wild and indigenous stock essentially unaltered by hatchery supplementation and occupies habitat that has been largely undisturbed by anthropogenic influences (Thurow 2000, Malison and Baxter 2010). Current Chinook Salmon runs (2012 n=145, R. Thurow 2013 unpubl data) are significantly lower than historic numbers, but these numbers represent an increase from the previous decade (Brown 2002, Holecek et al. 2009, Courbois et al. 2008). Adult Chinook Salmon returning from the ocean at ages 3 to 5 years generally arrive in Big Creek in late July and complete spawning by early September, although timing can vary between the upper and lower portions of the watershed (Kiefer et al. 2002, Isaak and Thurow 2006, Hamann et al. 2013). This timing coincides with steady baseflow conditions in the area that have facilitated consistent data collection on redd locations (Isaak and Thurow 2006). Spawning activity is concentrated in patches along the mainstem of Big Creek and in Monumental Creek, the largest tributary, where habitat is most suitable for spawning (Isaak et al. 2003, Thurow 2011, Hamann and Kennedy 2012).

The wilderness characteristic of the Big Creek watershed makes it an ideal system in which to gain an understanding of baseline stable isotope composition of stream biota in inland headwater streams and their relationship to catchment-scale environmental factors, especially since it is characterized by native anadromous salmon populations and a natural fire regime. The significant distance from the ocean (>1200 river kilometers) enables the ruling out of potentially confounding coastal effects on isotopic compositions. The mosaic of diverse geology, wildfire history, stream sizes, and salmon spawning activity facilitated the investigation of natural isotopic patterns across space and enabled evaluation of both physical and biological drivers of isotopic variation at the regional scale.

Spawning Densities

Salmon spawning densities were calculated from aerial redd surveys performed during the first week of September in 2011 and 2012 by the U.S. Forest Service Rocky Mountain Research Station (USFS RMRS) as part of a long term monitoring project (Isaak and Thurow 2006, Thurow 2011). Data were provided in number of redds per stream segment, the boundaries of which were predefined by USFS RMRS (R. Thurow, unpubl. data). Adult salmon spawner density (D) in fish m^{-2} was calculated for stream segments similarly to Verspoor et al. (2010) according to the equation:

$$\text{Salmon spawner density } (D) = \frac{R}{w \times l}(1.82)$$

where R is the total number of redds counted in the segment, w is the wetted width (in meters) at the downstream end of the segment during baseflow conditions in 2012, l is the length of the section (in meters), and 1.82 is the standard expansion factor used by NOAA – Fisheries and Idaho Department of Fish and Game for estimating the number of adult Chinook Salmon per redd (Beamesderfer et al. 1997). This is a conservative estimate according to fisheries biologists working in the Salmon River basin, but has not been assessed with empirical evidence (P. Kennedy, *pers. comm*).

Stream Water Chemistry

Bulk stream water samples were collected at every visit to each site in 2012 and 2013 in acid-washed amber bottles (Nalgene ChemClean, 120ml) after being rinsed three times at sampling location with stream water and kept cool until they could be frozen (<48 hrs).

All water samples were analyzed for total phosphorous (TP), total nitrogen (TN), nitrate, nitrite, ammonium, silicate and phosphate at the University of Washington (UW) Marine Chemistry Laboratory. Nitrate/nitrite, ammonium, phosphate and TN/TP were analyzed according to UW laboratory modifications of the cadmium reduction (Armstrong et al 1967), idophenol blue (Slawyk and MacIsaac 1972), molybdenum blue (Bernhardt and Wilhemls 1967) and persulfate digestion (Valderrama 1981) procedures, respectively, and are reported in µg/L.

Environmental variables: canopy cover, discharge, temperature, riparian vegetation, fire, geology and land cover

Canopy cover was estimated using a spherical concave densiometer (Forestry suppliers, Inc. No 43888). Readings were taken mid-channel in all four cardinal directions in mid-summer to capture the greatest extent of shading. Discharge measurements were made via velocity-depth profile transects at each site visit using a MarshMcBirney (Flo-Mate 2000) flow meter and reported in cubic meters per second (cms). Temperature (°C) was recorded at each site visit using a conventional mercury-free water thermometer. Riparian vegetation species data and percent cover for all cover types was collected along the riparian zone 50m upstream of every sampling location in September 2012.

Using a geographic information system (GIS) geodatabase (ArcMap 10.1; Environmental Systems Research Institute, Redlands, California) drainage area for each subbasin was calculated from USGS National Elevation Dataset 30m Digital Elevation Maps using sampling locations to define watershed boundaries. Overlay analyses determined geologic, wildfire, and land cover characteristics of each subbasin (Figures 3, 4, 5). Influence of fire was determined for each subbasin based on publicly available fire atlas data (Morgan et al. 2008) and presented as percent burned by year including all wildfires from 2000-2012. Geologic and land cover characteristics are presented as percent major rock type (Lewis 2012) and dominant land cover type (Fry 2011b), respectively. For these environmental variables, percent of subbasin major rock type as quartzite (% quartzite), percent of subbasin land cover as evergreen forest (% evergreen forest) and percent of subbasin burned since 2000 (% burn) were used as the predictor variables in subsequent analysis.

Macroinvertebrate and Periphyton Sample Collection

Macroinvertebrate and periphyton samples for stable isotope analysis were collected during the summers of 2012 and 2013 from riffle habitat at each of the 16 sampling locations (Figure 1). Sampling of all sites occurred within a seven-day period in mid-July, mid-August and mid-September, capturing conditions before the arrival of spawning salmon, during spawning and after peak spawning. Remote access and resources prevented mid-season (August) sampling at the three most remote sites (MON, BAM, BBM) in 2012. Macroinvertebrate samples were collected using a HESS Surber sampler (0.09-m^2, 243-µm mesh). Three locations across the width of the stream were sampled in aggregate to get a representative sample. The collections were rinsed with stream water, decanted to remove inorganic sediments, and then stored in 70-80% ethanol (EtOH) in glass vials until transport back to the laboratory. I did not attempt to quantify biomass, productivity, or diet of the aquatic biota.

Three macroinvertebrate taxa (*Heptageniidae, Hydropsychidae* and *Perlidae*) were identified under magnification to family according to Merritt and Cummins (1996), cleaned of any sediment, algae particles and other debris under the microscope before being prepared for stable isotope analysis. These three families were chosen based on their common presence across sites, adequate biomass for isotopic analysis, taxonomic diversity and difference in feeding strategies. *Heptageniidae* are grazing mayflies (Ephemeroptera) that feed primarily on biofilm attached to the rocks, *Hydropsychidae* are net-spinning caddisflies (Tricoptera) that feed primarily on organic debris particles suspended in the water column, and *Perlidae* are predatory stoneflies (Plecoptera) the feed primarily on smaller macroinvertebrates (Giller and Malmqvist 1998, Merritt and Cummins 1996). These taxa are used to represent grazers, collectors, and predators, respectively, in this study and area subsequently referred to as such.

In some studies, ethanol has been shown to influence the stable isotope ratios in aquatic invertebrates, increasing δ^{15}N values (~0.39‰) and decreasing δ^{13}C values (~1.18‰) (Ventura and Jeppesen 2009). There is no scientific consensus regarding the reliability or relative importance of this potential bias, and some suggest that effects are minimal, or are greater in certain taxa than others (Hobson et al. 1997, Sarakinos et al. 2002, Lau et al. 2012). Particularly relevant to this type of ecosystem study is the finding that changes in N, C, and especially S stable isotope values from preservation may be insignificant compared to changes expected from natural fractionation processes (Edwards et al. 2002). For example, Syväranta et al. (2007) found no significant differences between ethanol-preserved samples and those that were immediately analyzed.

More research into the methodology of stable isotope sample collection, preservation, and preparation from aquatic systems deserves continued attention and caution should always be taken in comparing stable isotope values across studies. However, given the nature of this study—the remote backcountry setting and long distance from full lab facilities—preservation was a necessity. Formalin is an alternative preservation technique that does not systematically affect $\delta^{34}S$ values (Edwards et al. 2002), but has been shown to significantly deplete ^{13}C and ^{15}N (Hobson et al. 1997) and generally is not a common technique for macroinvertebrate preservation (Syväranta et al. 2007). Acidification has also been used inconsistently in stable isotope sample preparation as well, but can have significant negative impacts on the validity of carbon, nitrogen and sulfur analyses (Bunn et al. 1995, Bosley and Wainright 1999, Connolly and Schlacher2013). Prioritizing consistency, 70-80% ethanol was used throughout the study for preservation of macroinvertebrates.

For periphyton samples, four to six rocks were collected from representative locations in the wetted channel of the riffle, scrubbed on all surfaces with a wire brush and rinsed with local stream water to remove all periphyton material (attached algae and associated microbes and detritus). The aggregate solution was shaken to homogenize the sample and pre-filtered through 500µm mesh to remove any coarse particulate material, sediment and invertebrates. A subsample of the pre-filtered solution was filtered directly onto pre-ashed glass fibre filters (Whatman GF/F 0.7-µm) using a PVC handheld vacuum pump and manifold until filters clogged, then stored in opaque foil packets to avoid further exposure to light, and kept cool until they could be frozen (<48 hrs). The remainder of the periphyton solution was stored in Whirlpaks with no headspace and stored similarly until frozen for subsequent stable isotope analysis if needed.

Stable Isotope Analysis

Periphyton and macroinvertebrate samples were dried at 60°C for 24 hrs. Whole body samples and multiple individuals of the same macroinvertebrate family from a sample were combined to ensure adequate biomass and control for variability between individuals. Samples were ground with mortar and pestle to a fine homogenous powder, and then subsamples were weighed and packed separately for carbon/nitrogen analysis (0.4 ± 0.1mg) and sulfur analysis (2.5mg ± 1.0mg). One quarter (25%) of the periphyton material was scraped off each filter and packed for carbon/nitrogen analysis (4.0-26.0mg). Remaining periphyton material (75% of filter surface area) was packed for sulfur analysis, but laboratory results indicated poor chromatography. Samples were combusted in an elemental analyzer (ECS 4010, Costech Analytical, Valencia, CA) into gases (N_2, CO_2, or SO_2), separated in a gas chromatography column and analyzed with a continuous flow isotope ratio mass spectrometer (Delta Plus XP, Thermofinnigan, Bremen, Germany) at the Washington State University Stable Isotope Core Laboratory.

Stable isotope ratios (the ratio of heavy isotope to light isotope, *R*) are reported as values relative to a standard according to the equation:

$$\delta^{15}N,\ \delta^{13}C,\ \text{or}\ \delta^{34}S = \frac{R_{Sample} - R_{Standard}}{R_{Sample}} \times 1000 \quad \text{(Farquhar 1982).}$$

The standard for N (nitrogen) is atmospheric N_2, for C (carbon) is Vienna PeeDee Belemnite (C_{VPDB}), and for S (sulfur) is Vienna Cañon Diablo Troilite (S_{VCDT}). All values are reported as per mille (‰) relative to these internationally recognized standards. Higher values of δ^{15}N, δ^{13}C or δ^{34}S thus indicate higher proportions of the heavier isotope in the sample. Analytical error associated with isotopic measurements of periphyton was 0.20‰ for δ^{15}N and 0.80‰ for δ^{13}C. Analytical error associated with macroinvertebrate isotopic measurements, evaluated from duplicate and triplicate samples, was 0.29‰ for δ^{15}N, 0.25‰ for δ^{34}S and 0.46‰ for δ^{13}C. Internal precision reported from the laboratory was approximately 0.06‰ SD.

Statistical analysis

Prior to statistical analysis, data were scaled and tested for compliance with basic ANOVA assumptions of normality and equal variance. Periphyton and grazer δ^{15}N data deviated from normality (Shapiro-Wilks: $p = 0.034$ and $p = 0.0023$, respectively). After transformations the data were still not normal, but the original data did not violate the assumption of homogeneity of variance. This is not uncommon in stable isotope studies (Mateo et al. 2008, Duda et al. 2011) so I proceeded with scaled δ^{15}N data as in Ramsay et al. (2012).

The importance of all twenty predictor variables (see Figures 8, 9, 10) was assessed using a classification and regression random forest model, which is robust with non-parametric data and a large number of predictor variables (Cutler et al. 2007). Relative importance of variables was evaluated by rescaling the percent increase in mean square error from 0 to 100% variability explained by each individual variable as in Kwon (2012). $\delta^{15}N$, $\delta^{34}S$ and $\delta^{13}C$ values were analyzed separately via a three-way ANOVA including time, site and taxa as main effects as well as two-way and three-way interactions with all components treated as fixed factors. Further investigation on taxon-specific responses was conducted with two-way ANOVAs. Interannual variability of $\delta^{15}N$ and $\delta^{13}C$ values was assessed for all three macroinvertebrate taxa and periphyton sampled at the same sites and weeks of 2012 and 2013 via simple linear regression. Long-term year effects were evaluated with macroinvertebrate C and N stable isotope data from 2007 at 3 of the sampling locations (UBC, BBT and RSH) collected during a previous study (B. Kennedy and K. Cromwell, unpubl. data). ^{34}S isotopic composition of biota was only analyzed in 2012 due to sample prioritization and budget limitations so year effects were not assessed for sulfur.

I conducted a principal component analysis (PCA) on centered and standardized environmental variables to examine the structure of the data and reduce dimensionality in the biological and physical landscape characteristics. The first three principal components were retained based on standard deviations greater than one (Quinn and Keough 2002) and cumulatively explained 73.7% of the variance (Table 1). The first axis (PC1=36%) was strongly correlated to several environmental variables indicative of stream water nutrients and productivity (highest PC loadings: TP=0.36, TN=0.34, NO_2=0.33, NO_3=0.33). The second axis (PC2=24.3%) was strongly correlated to several measures related to stream size (baseflow discharge=0.39, width=0.38, drainage area=0.37, elevation=-0.37) and cross-correlated with salmon density (-0.39). The third axis (PC3 = 13.4%) was strongly correlated to a variety of other variables that were more difficult to interpret (stream water phosphate=0.47, stream water silicate=0.44, % quartzite=-0.42). I selected total nitrogen (TN), baseflow discharge, and percent of major rock type as quartzite in subbasin (%quartzite) to include in subsequent regression analyses based on their eigenvalues in these results and on their interpretability. I also included percent cover at sampling location (%cover) and percent of subbasin burned since 2000 (%burn) in subsequent analyses because they had high loadings in PC4 and aligned with original hypotheses.

Multiple linear regression models were created to evaluate the relative importance of physical (%cover, discharge, % burn) and chemical (TN, %quartzite) environmental characteristics in predicting stable isotope ratios of periphyton and macroinvertebrates. We ran a tree model to evaluate for interactions, and with no evidence of possible interactions, we employed an additive regression model. Data were transformed according to box-cox power transform lambda values prior to running the models for each taxa-isotope combination. We developed a group of candidate models, including a global model of the five explanatory variables identified above and several reduced models guided by AIC forward backward selection methods. The relative importance for each predictor variable in the models was found using 95% bootstrap confidence intervals. Akaike information criterion, corrected for small sample sizes (AICc), was used for model selection (Burnham and Anderson 2002). Best fit and candidate models were identified using AIC weights (w_i) and when there was substantial evidence for use of a competitor model (ΔAIC < 1) I considered the F-values of all competing models before conclusions and interpretations were made. All statistical analyses were run using R statistical software version 2.14.2 (R Development Core Team; http://www.r-project.org/) and significance was evaluated at $\alpha = 0.05$.

Results

Site characteristics

Chinook Salmon spawner densities in 2012 ranged from 0 (in tributary stream sites LOG, CBN, CAV, PIO and CLF) to 0.008 fish m^{-2} (in upper Big Creek sites BAL, BBL and UBC). Density patterns throughout the watershed were significantly correlated between 2011 and 2012 ($r^2 = 0.99$, $F_{1,46} = 7060$, $p < 0.0001$) (Figure 6) and numbers are overall much lower than in most studies that explore the influence of spawning salmon on isotopic composition of periphyton and macroinvertebrates, even in the Pacific Northwest of the United States (Figure 7).

All streams sampled in this watershed were oligotrophic in nature. Total phosphorous (TP: ±4.0 µg L^{-1} to ±37.9 µg L^{-1}) and total nitrogen (TN: ±16.5 µg L^{-1} to ±498.7 µg L^{-1}) were positively correlated ($r^2 = 0.43$). All forms of nitrogen in stream water samples (TN, NO_2^-,

NO_3^-, NH_4^+) were highly correlated and had similar loadings in the PCA analysis (Table 1). Total nitrogen and phosphorous concentrations were unusually high in three tributary streams in the lower basin (CLF, PIO and RSH). CLF and PIO had TN concentrations that were an order of magnitude higher than many of the other sites. While a mechanism for this pattern has not been identified, it is consistent with findings from other studies on these same streams (Sanderson et al. 2009, Davis and Minshall 1999).

The drainage area corresponding to each of my sites ranged from ±19 km^2 to ±1462 km^2 and captured a range of wildfire history (0% - 44% of drainage area burned since 2000), land cover type (16% - 77% evergreen forest), geologic composition (0% - 94% quartzite as major rock type). Sampling sites were located in a range of 2nd to 5th order streams with baseflow discharge ranging from 0.02 cms to 5.98 cms and a various degrees of shading (0% - 87% cover at sampling location). Site and corresponding subbasin characteristics are summarized in Table 2.

Site, month, year and taxa as sources of isotopic variability

Taxa and site were consistently the most important of the twenty original predictor variables in explaining variability in stable isotope ratios for nitrogen (taxa: 30%, site: 9%), carbon (taxa: 12%, site: 9%), and sulfur (taxa: 11%, site: 11%) (Figures 8, 9, 10). A three-way ANOVA including site, taxa and month further confirmed that taxa ($F_{(3,187)}$=301.49, $p <$ 0.0001) and site ($F_{(15,187)}$=24.82, $p < 0.0001$) significantly affect $\delta^{15}N$ values in this system but month does not ($F_{(2,187)}$=3.68, $p = 0.0503$). The two-way interaction between site and taxa was significant ($F_{(44,187)}$=3.59, $p = 0.004$) indicating that the site effect may not be consistent across all taxa. Given that nitrogen stable isotope ratios of pooled taxa and sites were significantly different from each other (ANOVA, $p < 0.0001$) (Figure 11), I conducted a two-way ANOVA for each taxa, with site and month as fixed effects, to evaluate relative importance of time and space across individual trophic levels (Table 3). Site was the only significant effect for periphtyon ($p < 0.001$). Site and month ($p < 0.001$, $p = 0.04$) were significant for grazer δ^{15}N values. Site, month, and the interaction term were all significant for predator δ^{15}N values ($p = 0.002$, $p = 0.02$, $p = 0.03$, respectively). There were no significant effects for collector δ^{15}N values. All ANOVA models were evaluated for compliance with assumptions of normality and homogeneity of variances via graphical diagnostics.

Similar analyses evaluating the effects of taxa, site and month on δ^{13}C and δ^{34}S values were also performed. For carbon, all effects except for the three-way interaction were significant (Table 4) and for each individual taxa site was a significant main effect, and month was an additional significant effect for all except predators (Table 3). The only significant effects overall for sulfur were taxa and month (Table 4), but when evaluated by individual taxa, site was highly significant for grazers, collectors (also site x month interaction effect) and predators (Table 3).

The temporal variability in ^{15}N isotopic ratios varied slightly by site, but was overall quite low (range: 0.2‰ at BBM — 3.7‰ at PIO) (Table 5). There was a significant relationship between stable isotope ratios of taxa sampled at the same locations in consecutive years for nitrogen and carbon (r^2 = 0.675, 0.667, respectively) (Figure 12, 13). This relationship was very consistent for δ^{13}C values of each taxa between 2012 and 2013 data (r^2 = 0.62: periphyton, 0.77: grazers, 0.57: collectors, 0.82: predators). The relationship for δ^{15}N values was strongest for grazers (r^2 = 0.83), followed by collectors (r^2 = 0.57), periphyton (r^2 = 0.42) and predators (r^2 = 0.23). δ^{15}N data for macroinvertebrates was consistent between other consecutive years as well (2006 & 2007, r^2 = 0.814) and longer time scales (2007 & 2012, r^2 = 0.912) (Figure 14).

Relationship between periphyton nitrogen isotope ratios and higher trophic levels

Periphyton exhibited the least amount of variability (mean range = 0.6‰), followed by grazers (mean range = 0.7‰), predators (mean range = 0.9‰), and collectors exhibited the greatest variability (mean range = 1.7‰) (Table 5). Site-specific mean δ^{15}N values of periphyton strongly predict that of grazers (r^2 = 0.84, $p < 0.0001$), show a weaker but still significant relationship with that of predators (r^2 = 0.32, p = 0.02), and do not show any association with the mean δ^{15}N values of collectors (r^2 = 0.03, p = 0.23) (Figure 15).

Nitrogen stable isotope ratios follow expected patterns of enrichment through trophic levels in this watershed (mean and median δ^{15}N values of periphyton < grazers < collectors < predators) (Figure 11). Although the taxonomic pairs do not necessarily represent complete steps in trophic position, observed discrimination (Δ) was well below the common literature value of 3.4‰ per trophic level (Figure 16). Significant differences existed between pairs (one-way ANOVA, $F_{(3)}$ = 11.69, $p < 0.0001$). Mean $\Delta^{15}N_{\text{Grazer-Periphyton}}$

(1.1‰) was similar to mean $\Delta^{15}N_{\text{Predator-Collector}}$ (1.1‰) and both pairs exhibited slightly less discrimination than $\Delta^{15}N_{\text{Predator-Grazer}}$ (2.2‰) and significantly less discrimination than $\Delta^{15}N_{\text{Predator-Grazer}}$ (3.2‰), reflecting expected differences in the trophic distance from each other (Figure 16). Observed trophic discrimination was not significantly different between sites (one-way ANOVA, $F_{(15)} = 0.495$, $p = 0.924$) nor between sites with different levels of salmon density (ANOVA, $F_{(2)} = 0.186$, $p = 0.831$).

Relative influence of environmental factors

The most important environmental characteristics in predicting nitrogen stable isotope ratios for three of the four taxa were percent of watershed burned and baseflow discharge (AIC model selection: $w_i = 0.34 - 0.61$) as indicated by the top models (Table 6). This final model explained 30% of the variation in periphyton $\delta^{15}N$ values ($p = 0.0011$), 42% of the variation in grazer $\delta^{15}N$ values ($p < 0.0001$) and 50% of the variation in predator $\delta^{15}N$ values ($p < 0.0001$). Percent of watershed burned since 2000 (%burn) was the variable with the most explanatory power across all taxa, and was the only parameter in the top model for collectors ($w_i = 0.59$) and positively correlated to mean $\delta^{15}N$ values among all taxa ($r^2 = 0.34$). The positive linear relationship was strongest for predators ($r^2 = 0.54$) and decreased in strength as trophic level decreased (collector: $r^2 = 0.25$, grazer: $r^2 = 0.17$, periphyton: $r^2 = 0.13$). Baseflow discharge, as a metric of watershed and stream size, was the second most important predictor in the model set (Table 7). It was slightly positively related to mean $\delta^{15}N$ values in periphyton ($r^2 = 0.09$), grazers ($r^2 = 0.27$), and predators ($r^2 = 0.06$), and had no relationship to that of collectors ($r^2 < 0.001$) (Figure 22b). While the top models for periphyton and grazers also included TN and %quartzite, respectively, the two-parameter model was a highly competitive candidate (ΔAIC < 0.4) and the F-value was higher for the two-parameter model for both taxa (Table 6). To facilitate interpretation I selected the two-parameter model for all four taxa.

For δ^{13}C values, the global model was the top model for predators. The top model for periphyton and grazers were identical, including all parameters except % cover, while the top model for collectors included only baseflow discharge and TN. There was little variability in the model fit for each taxon (range: $R^2 = 0.54$ for collectors – $R^2 = 0.63$ for predators) and this is likely because the high degree of parameter inclusion in these models (Table 8). Multiple linear regression model results predicting δ^{34}S values were less consistent across taxa than for ^{15}N and ^{13}C. Adjusted R^2 values for these models were more variable as well (range: $R^2 = 0.35$ for grazers – $R^2 = 0.78$ for predators). The top model for grazers and collectors was identical, comprising two parameters: baseflow discharge and % quartzite. The global model for predators had the lowest AIC, but there was substantial support for two alternative models ($\Delta_i = 0.41, 0.55$) that dropped % cover or %cover and % burned, respectively (Table 9).

Spawning salmon influence

Contrary to expectations, sites with the highest spawner densities in our study (still relatively low at 0.005—0.008 fish m^{-2}) had significantly lower δ^{15}N values (mean ± SD:

1.0‰ ± 0.7) among all taxa and months compared to sites with low spawner density (0.0001—5.3×10^{-5} fish m^{-2}, $\delta^{15}N$: 2.7 ‰ ± 0.8) and no salmon ($\delta^{15}N$: 1.9‰ ± 0.9). $\delta^{15}N$ values of biota in sites with no salmon did not differ from low spawner density sites ($F_{(2)} = 16.34$, $p < 0.0001$; Tukey HSD: $p > 0.05$). This pattern was true for each individual taxon as well (Figure 17). $\delta^{34}S$ values were significantly different at sites with no salmon compared to sites with low or high spawner densities (one-way ANOVA, $F_{(2)} = 42.4$, $p < 0.0001$, Tukey HSD: $p = 0.67$). This pattern held for pooled taxa and for each individual taxon (Figure 18).

In the headwater reaches of Big Creek at our site with the highest spawner density (BAL) only periphyton and predators were more enriched in ^{15}N (by 0.75‰ and 0.84‰, respectively) relative to the reference site LOG in Logan Creek, the neighboring stream with similar landscape characteristics but no salmon (Figure 19a). This difference was small (<1‰) and insignificant ($F = 1.89$, $p = 0.162$). Carbon stable isotope composition did not differ for pooled biota ($F = 0.198$, $p = 0.66$) or any individual taxon between these two sites in the upper basin (Figure 19b). Sulfur stable isotope ratios for all macroinvertebrate taxa were significantly different between these two sites (Figure 19c, $F = 271.2$, $p < 0.0001$). Highlighting the spatial differences observed in each element at this more local scale, a dual isotope plot of $\delta^{13}C$ and $\delta^{15}N$ values did not produce site separation at this paired watershed scale (Figure 20) while a similar dual isotope plot of $\delta^{15}N$ and $\delta^{34}S$ values revealed noticeable differences between these two sites across all taxa (Figure 21).

Discussion

Variation in δ^{15}N, δ^{34}S and δ^{13}C values of periphyton and macroinvertebrates

Understanding the mechanisms of isotopic variation in stream ecosystems can be a challenge for aquatic ecologists trying to identify specific patterns of resource use and movement. I quantitatively addressed this issue with a comprehensive field study of four aquatic taxa and three elements over two summers, explicitly analyzing the observed variability as well as apparent trends and environmental correlations. Here, I discuss the dominant drivers of isotopic variability and make recommendations to improve experimental design of future stable isotope studies in stream networks, provide system-specific data on the isotopic landscape of periphyton and macroinvertebrates in the Salmon River basin, Idaho, USA, and finally, offer rudimentary insight into environmental correlations.

Physical, chemical and biological variables previously evaluated for effects on N, C or S stable isotope ratios in aquatic stream biota were compiled from the literature. The initial quantitative assessment included twenty of these variables—capturing patterns and processes ranging from broad, catchment wide characteristics to local, site specific conditions—that collectively explained over 60% of the variation observed in N, C and S stable isotope ratios. I am not aware of another study that has simultaneously taken into account this many potential drivers of variation to evaluate the relative significance of each, or that has done so for all three elements.

In contrast to the results from many previous studies highlighting high temporal variability in periphyton and macroinvertebrates (Hadwen et al. 2010, Ishikawa et al. 012, Duda et al. 2011, Jardine et al. 2014), neither month nor year explained much of the variability in our dataset. Relatively few studies to date have considered the interannual variability of δ^{13}C and δ^{15}N in lotic systems (but see Duda et al. 2011, Maier et al. 2011), or other ecological systems more generally (but see Woodland et al. 2012, Gu et al. 1999, Drake et al. 2011, Leavitt et al. 2006, Randerson et al. 2002, Bowen 2010). Our study suggests little interannual variability for all taxa sampled, not only between consecutive years, but also across time scales as great as five years (Figures 12, 13, 14). This scale of temporal variation may be increasingly important to consider as stream ecosystem dynamics change in response to changing climate and as we employ new methods of assessing systemic changes.

Our study also indicates relatively little temporal variability existed at shorter time scales. Although significant seasonal variation between summer and winter has been observed in some systems (Ishikawa et al. 2012), the majority of stream ecology studies using stable isotope analysis are concentrated during the spring, summer and fall. Fieldwork was conducted in July, August, and September—when productivity is greatest and salmon are spawning in the streams. The observed isotopic stability through time may be partly a result of stability in other biological and environmental conditions during the sampling period. Some parameters previously shown to influence stable isotope ratios in lotic biota are strongly related to seasonality and do not vary dramatically during the summer months in this snowmelt driven system. For example, water velocity has been shown to affect δ^{13}C and δ^{15}N values of periphyton as a result of redox condition differences across stream habitat classifications (Trudeau and Rasmussen 2003, Finlay et al. 1999, Finlay 2001), but when flows are relatively stable over time—as they were in Big Creek during the study period—its observed effect on the isotopic composition of biota may be minimized. Previous observations of low δ^{13}C and δ^{15}N variability in streams with stable flows substantiate this explanation (Huang et al. 2013). Light, percent cover, and vegetation are also related to seasonality and did not vary dramatically at site locations during the sampling periods, potentially further reducing sources of variability and contributing to the insignificant temporal variation in this study.

I do not attempt to delineate specific mechanisms of variability here, but note that biological processes such as tissue turn-over, assimilation rates and transformation, and preferential use of specific amino acids also have the potential to influence isotopic composition and observed discrimination at shorter time scales. Nevertheless, the temporal consistency observed allowed me to treat multiple samples from the same site as replicates in further analysis and to focus on explaining the more significant sources of variability here: site and taxa.

Site and taxa consistently had the most explanatory power for all three elements and there was a substantial difference between the power of these and the next most influential variables (Figures 8, 9, 10). It was unsurprising that a large amount of the variation was explained by taxa given the unique trophic status and feeding strategy of each of the four target taxa. I nonetheless explicitly tested the common assumption that trophic level processes overshadow spatial and temporal variation according to Guzzo et al. (2011). Additionally, there have not been any studies I am aware of that assess the relative importance of space, time and taxa on sulfur stable isotope ratios. The primary importance of taxa in driving C, N and S stable isotope ratios supported the structure of subsequent analyses: assessing relationships between the different trophic levels represented and investigating drivers of isotopic composition for each taxon separately.

Relationship between periphyton nitrogen isotope ratios and higher trophic levels

I focused on the relationship between periphyton and aquatic macroinvertebrates that are potentially or partially reliant on in-stream production due to the predominantly autotrophic nature of the streams in this inland headwater system. Application of the gradient approach to quantify reliance of macroinvertebrate taxa on periphyton was effective in this study. Simple linear regression of mean δ^{15}N values of a consumer against its source reveals strong reliance on that food source if there is good fit and the slope is close to 1 (Rasmussen 2010). Site-specific mean δ^{15}N values of grazers were strongly correlated with their predicted food source, periphyton, and a less significant association was evident between predators and periphyton (Figure 15). Based on invertebrate behavioral knowledge, we do not expect the predatory macroinvertebrates (perlidae) to directly ingest periphyton (Merritt and Cummins 1996), so I infer that periphyton is only a resource valuable to predatory invertebrates indirectly through the food chain. The weaker relationship with predators is also expected since they are more generalist feeders; we expect them to be reliant on a more diverse set of food resources. Collectors, especially the net-spinning caddisfly (hydropsychidae) that I targeted, are opportunistic feeders that feed on organic matter suspended in the water column, little of which is expected to be periphyton, so the large amount of variability between collectors and periphyton also agrees with my expectations of inconsistent reliance on periphyton by collectors. The different relationships observed between taxonomic pairs are reasonable since the make up of suspended organic matter depends on location-specific characteristics (e.g. leaf litter inputs, disturbances, etc) whereas grazers and predators are more reliant on autotrophic periphyton resources that are attached to rock substrate surfaces across all sites.

Periphyton δ^{15}N values exhibited the least amount of site-specific variability on average. This result initially contrasts with that of other studies that suggest using primary consumers as an isotopic baseline because they are less variable than primary producers (Post 2002, Coat et al. 2009), but I point out that my results are explicitly addressing site-specific variability here, not system wide variability, and the range in grazer δ^{15}N values was greater that that of periphyton only at 9 of the 16 sites. This approach and its findings can improve future experimental design. For example, it will enable researchers to target the more variable sites if they are interested in investigating the variability itself, or appropriately select sites with less variability for more in-depth research on trophic relationships.

Observed discrimination of ^{15}N between trophic levels

While nitrogen stable isotope ratios in this watershed followed expected patterns of enrichment through trophic levels (Figure 11), observed discrimination in ^{15}N between individual trophic levels ($\Delta_{\text{consumer-diet}}$) was well below the value of 3.4‰ per trophic level that is commonly accepted and used, even in lotic studies (Kline 1990, Shin 2011). This is not surprising given the known variability in $\Delta_{\text{consumer-diet}}$ (1.3-5.3‰: Minigawa and Wada 1984, Post 2002, Adams and Sterner 2000, Vander Zanden and Rasmussen 2001) and recent research specifically finding lower values of trophic discrimination in lotic systems (Jardine 2014, Bergfur 2009, Goedkoop 2006). These results provide additional support against the widespread use of 3.4‰ as the standard enrichment per trophic level. For example, the mean δ^{15}N value of the macroinvertebrate predator (perlidae) was ±3.2‰ greater than that of periphyton. Using nitrogen trophic enrichment theory alone, one could misconstrue these results to indicate that the predator is one trophic position above periphyton. Common knowledge of feeding strategies for this taxa indicate that it feeds primarily on other invertebrates, rather than on basal, primarily autotrophic resources such as periphyton (Merritt and Cummins 1996). Along these lines, the grazer (*heptageniidae*) rely primarily on scraping or grazing periphyton material off of rock substrate, and yet on average were enriched in ^{15}N only 1.1‰ relative to periphyton. Future studies should make the additional effort to identify and incorporate more appropriate values of trophic discrimination when trying to extend mixing models to multiple trophic levels.

The causes of variation in observed discrimination between consumers and their diet and how this affects stream webs overall is complex (Bergfur et al. 2009). The observed trend of low $\Delta_{\text{consumer-diet}}$ in this study may be related to the oligotrophic nature of the streams sampled. Isotopic discrimination occurs during the conversion from source to product: lighter isotopes are preferentially converted to the product, as they are slightly more energetically reactive than their counterparts with higher atomic mass (Evans 2001). Discrimination is observed only when that reaction is incomplete because the remaining nitrogen in the source has a greater relative abundance of heavy isotopes than the product. If all nitrogen from the source gets converted into product, then no discrimination is apparent at all (Owens 1987, Evans 2001). Thus, in oligotrophic, N-limited stream systems where most source N is converted to product out of necessity, it is reasonable to expect a reduction in observed discrimination. This mechanism has been suggested as a driver of variability in observed discrimination in other N limited settings (Adams and Sterner 2000, Selbie et al. 2009) and is consistent with the low discrimination observed between all trophic levels in this study.

The nitrogen content of basal resources has also been shown to influence ^{15}N fractionation, primarily through an inverse relationship (Vander Zanden and Rasmussen 2001, Adams and Sterner 2000, Goedkoop 2006). Given the low nitrogen content of periphyton in Big Creek (0.25 – 18.3% N, C:N ratios 6.0-13.8) we might expect higher N^{15} fractionation than was actually observed (Adams and Sterner 2000). I could not explicitly evaluate that relationship because the samples in this study did not cover a wide range of

N content. However, I suggest that the narrow range in N content explains the relatively low variability in observed discrimination, especially between periphyton and grazers. Variation in discrimination rates may also be related to the specific trophic level investigated (Gannes et al. 1998, Vander Zanden and Rasmussen 2001, Cremona et al. 2010, Alp et al. 2013). I found that variability in $\Delta_{\text{consumer-diet}}$ was similar for grazers and predators (Figure 23). This agrees with results from Cremona et al. (2010) and Vander Zanden and Rasmussen (2001) that variability in observed discrimination may be more a result of organism type and metabolic processing than trophic position alone.

The consistent rate of ^{15}N enrichment through all four taxa across all sites suggests that observed discrimination is not impacted by spatially heterogeneous environmental conditions, although actual isotopic composition may be. Certain trophic levels sometimes benefit disproportionately from a nutrient subsidy if they have access to the nutrients sooner, through multiple pathways or are resilient to disturbances such as redd digging that generally accompany salmon derived nutrient subsidies (Wipfli et al. 1998, Hicks et al. 2005, Chaloner et al. 2002). Assessing the δ^{15}N values across trophic levels and feeding strategies as I did, with little variation in observed discrimination across sites, I conclude that none of our target taxa are 1) impacted disproportionately by the diverse environmental conditions (gradients of background nutrient concentrations, productivity, wildfire history, salmon presence and density, etc) or 2) utilizing isotopically distinct nutrient sources across sites. This finding increases certainty that the pattern observed across space in one taxon will likely reflect that of other taxa, even in the face of spatially distinct conditions.

Regardless of the precise mechanisms responsible for the observed discrimination in ^{15}N between taxonomic pairs in this study, I have clearly demonstrated low $\Delta_{\text{consumer-diet}}$ between taxa that are indirectly and directly connected in lotic food webs. These findings are in line with other observations of lower and more variable trophic fractionation in lotic systems and at the lower end of the food web (Bunn et al. 2013, VanderZanden and Rasmussen 2010, Goedkoop et al. 2006). Furthermore, I have shown that there is consistency in trophic discrimination patterns across sites despite significantly different δ^{15}N values in the basal resource and a variety of environmental conditions, including external pulsed salmon subsidies. I acknowledge that other mechanisms of nitrogen incorporation are not specifically addressed in this study (N-fixing plants, turnover rates, etc) and I did not attempt to isolate specific diet-consumer pathways. Nevertheless, the spatial and temporal scope combined with the diversity of trophic guilds and environmental conditions evaluated does capture much of the inherent variability.

Spatial variability: Environmental correlations in stable isotope composition of periphyton and macroinvertebrates

All taxa and isotope combinations (except collector δ^{15}N values) showed significant site effects, agreeing with other studies that have identified spatial variability in isotopic composition, especially at lower trophic levels and in lotic environments. One major contribution of stable isotope analysis to this ecological field is in the creation and refinement of mixing models, which are then used for trophic position estimation or resource use partitioning. The selection of taxa or trophic level to use as an isotopic baseline in these mixing models has implications for their results, and may require corrections that account for spatial variation in the basal resource (Vander Zanden and Rasmussen 1999). Primary consumers have been heavily favored in defining isotopic baselines in many recent studies because primary producer $\delta^{15}N$ values are generally deemed too variable to constitute a steady baseline (Vander Zanden and Rasmussen 1999, Post 2002). With the quantitative understanding of the spatial scale of variation in primary producers that I provide, however, it is possible to develop a shifting baseline that incorporates spatial differences and improves trophic position estimations (Woodcock 2012). A similar approach has been developed and employed for addressing temporally dynamic baselines in isotope mixing models (Woodland et al. 2012). As this approach develops, identifying the primary sources of variability is an important step in stable isotope mixing model studies to determine the scale (local, regional or global) and the type (time or space) of corrections to employ before sound interpretations can be made. The predictive relationship between periphyton $\delta^{15}N$ values and that of grazers and predators discussed earlier further denotes the potential for improved isotopic baseline calculations using basal resources if between-site variability is included.

The target taxa in stable isotope studies should also be chosen to reflect specific research questions. Results from the collector taxa highlight this; while periphyton revealed site-specific differences, collectors did not have significant differences across space or time at the scales I explored. While the higher variability across time and space observed in collectors might decrease their utility for within-system comparisons of resource use, taxa of this nature may become useful in comparisons across distant ecosystems. Whereas this is generally warned against, I point out that the lack of significant site and time effects in collectors suggests that they may be integrators of large-scale watershed conditions and processes, a fact that may be useful by enabling corrections and comparison factors between disparate systems. My research sought to answer calls for more research coupling the two realms of stable isotope composition and spatially distinct environmental factors, including multiple factors simultaneously and focusing on nitrogen and sulfur isoscapes (Polis et al. 1997, Trudeau and Rasmussen 2003, Davis et al. 2013). The finding that variability between sites was greater than the changes observed within sites over the course of the season will enable future research to quantify the spatial scale at which stable isotopes of periphyton and macroinvertebrates vary.

The positive relationship between δ^{15}N values of all taxa and the percent of the catchment area that has burned since 2000 (Figure 22a) suggests that the isotopic nature of nitrogen sources and/or processing is altered with wildfire activity. Spencer et al. (2003) found elevated macroinvertebrate δ^{15}N values at fire-impacted sites in Glacier National Park, Montana, and proposed that autochthonous food sources became more enriched after fire and that other trophic levels became increasingly reliant on this food source. I found periphyton δ^{15}N values were higher in the lower portions of the watershed, where fire activity has been much more prevalent in the last 12 years. I cannot determine if fire is the ultimate cause for the observed enrichment relative to unburned areas, but notably, the correlation is consistent across time, space and taxa. Wildfire can alter thermal conditions (Rhoades et al. 2011), flow (Davis et al. 1999, Arkle et al. 2010), riparian vegetation communities (Jackson and Sullivan 2009), macroinvertebrate community composition (Mihuc et al. 1996, Minshall et al. 2001), leaf litter break down rates (Koetsier et al. 2010), nitrogen dynamics (Stephan et al. 2012) and scouring (Minshall et al. 2001) in Western mountain streams (Isaak et al. 2010), any of which may be indirectly responsible for isotopic changes in the biota as well. These fire effects may be apparent in streams more than five or ten years after the fire in some systems (Minshall et al. 1989, Gresswell 1999), and my results suggest changes in stable isotope composition of the aquatic biota can persist for long time periods as well. The isotopic nature of fire-impacted streams may help identify these subtly persistent effects in lotic nutrient dynamics. Future research on this subject should consider the specific metric used for fire activity to determine if the significance of this explanatory variable is driven by overall percent of catchment area burned (this study), by time elapsed since fire, or by the severity of fire.

The relationship between δ^{15}N values and stream size was not strong (Figure 22b), but baseflow discharge (my metric for stream size) was an important model parameter (Table 6). This coincides with findings that δ^{13}C of periphyton has a strong relationship to watershed size (Finlay 2001). In situ productivity can vary significantly in streams of different sizes due to light availability, nutrient inputs from flooding, keystone species activity, terrestrial leaf litter inputs and N-fixing plant abundance (Helfield and Naiman 2006, Naiman et al. 2002, Hocking and Reimchen 2009), which may in turn influence nitrogen dynamics and δ^{15}N values of primary producers and consumers in the stream (Compton et al. 2003, Adams and Sterner 2000). Productivity should be explicitly evaluated in future studies quantifying natural isotopic variability in streams of different sizes to determine potentially confounding effects. I recommend future experimental designs take these results into account and avoid comparing isotopic values across streams of different sizes, recognizing that spatial variation likely results from a combination of multiple biogeochemical factors and complex processes that will take time to unravel.

Overall, a mechanistic understanding of why sites in the upper basin, which are generally smaller and less burned, have lower δ^{15}N values is warranted. Similarly, investigations into the ultimate cause of site differences in δ^{34}S values in stream biota are encouraged. Because baseflow discharge and % quartzite were the two parameters common in the top model predicting sulfur stable isotope values of each macroinvertebrate taxa (Table 9) I direct future research to focus on underlying geologic differences and the pathways for sulfur uptake in headwater systems. Finally, while the R^2 values of each top model, for N and S, indicate that some unexplained variation remains, this is to be expected in ecological studies and especially given the multitude of factors that have been shown to influence stable isotope ratios in lotic biota studies in various locations, spatiotemporal scales and conditions.

Utility of nitrogen and sulfur in detecting marine derived nutrients at different scales

The drivers of nitrogen and sulfur stable isotope ratios have particularly important implications for marine derived nutrient (MDN) studies. Reported δ^{15}N and δ^{34}S values of adult spawning salmon are significantly higher than the values of locally derived nutrients in headwater systems (Kline et al. 2007, Fry and Sherr 1984, Peterson and Fry 1987), so if marine derived nutrients do subsidize lower trophic levels in the streams we expect to see isotopic enrichment (increased δ values) in the biota at sites where salmon were present relative to salmon-free sites. Surprisingly, I observed the opposite pattern when comparing isotope values across the Big Creek watershed; I found that neither nitrogen nor sulfur stable isotope ratios indicated incorporation of MDNs into periphyton or macroinvertebrates via isotopic enrichment at salmon sites. I offer a few different explanations for this unexpected observation, and note there is the possibility that MDNs are becoming incorporated but were not detected in this study as a result of insufficient spatiotemporal resolution or target taxa. More likely however, these results are a valid indication that MDNs are not incorporated at a detectable level into the local in-stream biota in this system because 1) the spawning densities occurring in this region are lower than any other study I know of explicitly investigating MDN use (Figure 7), 2) the amount and quality of nutrients remaining in the salmon that travel this far inland may be quite low, and 3) I have observed carcasses removed by scavengers, such as by bears, thereby removing them from direct contact with the stream and eliminating the potential for direct pathways of incorporation into lower trophic levels in the stream.

Importantly, my results are consistent at different spatial scales. Across the entire watershed, the lowest $\delta^{15}N$ values occurred at the sites with greatest spawner density, but these sites are all concentrated in the headwater portions of Big Creek. Analyzing within this upper basin, I compared my site in Big Creek (BAL; above the Logan Creek confluence) with a reference site in Logan Creek (LOG) because the two subbasins are comparable in drainage area, elevation, burn history, and land cover, but differ in bedrock geology and salmon presence/absence. Logan Creek has no salmon while this portion of Big Creek has the highest spawner density in the watershed (see Table 2). The mean $\delta^{15}N$ values of each taxon in BAL were slightly higher than their counterparts in LOG but this was not statistically significant. The inherent variability was greater than any difference that could be explained by the presence of absence of salmon.

The $\delta^{34}S$ values of each taxon in BAL were significantly lower than in LOG, again contrary to expectations of enriched sulfur content in adult salmon returning from the ocean environment. Bedrock geology is very different in the LOG and BAL subbasins: dominated by granodiorite (82%) and rhyolite (72%), respectively. Quartzite comprises 16% of the major rock type in the Logan Creek watershed and is not present in the BAL subbasin. Quartzite is composed almost entirely of silicate and, while it is generally considered insoluble to chemical weathering (Drever 1997), this difference in basal chemical resources available to the biota (fungi, soil microbes, etc) may be partially driving the pattern observed in the stream biota.

Results also indicate the utility of sulfur stable isotopes in resource partitioning studies as it greatly improved the ability to separate samples from different locations (Figure 20 and 22). Improved separation was found in marine food webs utilizing sulfur and carbon stable isotopes (Connolly et al. 2004, Fry et al. 2002). I extend this method to freshwater systems, but found the combination of nitrogen and sulfur to provide the best separation.

These findings at smaller spatial scales support my original hypothesis that a multitude of environmental conditions in a catchment may simultaneously influence background nutrient sources, processes, and the resulting patterns in stable isotope ratios in the biota. In this study, I do not identify the mechanistic pathways of nitrogen or sulfur use and so cannot determine whether there is in fact no MDN influence or if it is just overshadowed in the isoscape by other more dominant environmental conditions. This would be a topic to explore more with future research, but it is equally important to recognize that the end result and its implications on fisheries management is the same: there was no evidence of nutrient feedback loops between adult salmon and in-stream biota via elevated ^{15}N or ^{34}S ratios in this inland headwater system that has supported wild salmon populations for centuries. The effects of large salmon runs have been quantified in stream water nutrient loads (TP, TN), in productivity (chlorophyll a, AFDM), in whole-stream metabolism, and in periphyton and macroinvertebrate δ^{15}N (Holtgrieve et al. 2011). If similar isotopic enrichment occurred in inland systems with low spawning numbers, then it would be reasonable to infer similar responses in productivity and whole-stream processes in response to salmon spawning. However, this investigation revealed other factors influencing the stream conditions and processes that surpass the influence of spawning salmon on periphyton and macroinvertebrate nutrient composition, with implications for ecosystem management.

I recommend that studies explicitly looking for isotopic evidence or ecological effects of marine derived nutrients incorporate environmental characteristics of the focal catchments in addition to local conditions such as light and velocity that are already commonly included. Specifically, I recommend at least one metric to account for physical attributes (e.g. size of the system, stream gradient), biological attributes (e.g. vegetation, salmon), relevant ecological processes (e.g. wildfire, anthropogenic activity) and chemical attributes (e.g. stream water nutrients, geology). Metrics ultimately chosen for inclusion should reflect the temporal and spatial scope of the project as well as hypotheses being tested. This recommendation is also applicable more generally to any ecosystem subsidy study.

Conclusions and Future Research

This study explicitly explored spatiotemporal variability in N, C and S stable isotope values of aquatic biota, trophic discrimination, and correlations with environmental factors in an inland, native salmon supporting watershed unimpacted by anthropogenic activity and subject to frequent natural wildfires. Results of this study indicate that in this oligotrophic stream network the N, C and S isotopic composition of periphyton and macroinvertebrates does vary considerably, but this variability can be attributed to a few major factors, specifically taxon and site. Spatial variability often confounds isotopic studies as it varies as a function of multiple factors, and through separate analysis of C, N, and S, I was able to determine the relative importance of a many potential driving variables. Focusing on the environmental correlations with N and S stable isotope ratios, I found that the conditions associated with small, unburned headwater streams strongly influence the nitrogen stable isotope composition of the aquatic biota, producing significantly lower δ^{15}N values than observed in the lower regions of the basin. Regional variability in bedrock geology may influence the biogeochemical nature of streams and sulfur stable isotope ratios of the biota therein. Size also drives variability in both sulfur and nitrogen isotopic ratios, with many possible mechanisms contributing to the observed trends.

It is my hope that the results presented here will help others analyze and interpret stable isotope data from Big Creek and the greater Salmon River basin, specifically in re-examining conclusions form previous studies, prompting analysis of existing but unpublished data, and by informing future efforts examining MDN incidence via stable isotopes. The finding that values are not highly variable during the summer or between years in this system will streamline future studies by reducing field sampling efforts and laboratory costs needed to capture isotopic conditions. The target taxa for future studies depends on the specific research questions, and should consider my findings that periphyton strongly reveals site-specific differences, grazers and predators are strongly linked to this autotrophic resource here, and that collectors do not have significant differences across space or time at the scales I explored due to the greater variability in their composition. I provide fundamental information on the spatial scale at which N and S stable isotope ratios can vary in different aquatic taxa, and suggest that spatial variability should be quantified and incorporated into shifting baseline calculations if mixing models are used to evaluate resource use in food webs.

Extra caution is recommended in the use sulfur and nitrogen to trace marine derived nutrients in the food web: I found effects to be non-existent or overshadowed by other environmental conditions when salmon populations are small and/or inhabit inland watersheds. I also recommend greater consideration of landscape level conditions (e.g. land use history, underlying biogeochemistry) as much as localized ones (e.g. velocity, light) and I emphasize that this is especially important when comparing across distances or disparate conditions within a region. Taking the time to identify and understand the nature of spatiotemporal drivers of isotopic variability in a study system will improve the quality of ecological conclusions and increase the reliability of stable isotope analysis as its use in biological and ecological systems continues to expand.

Figures

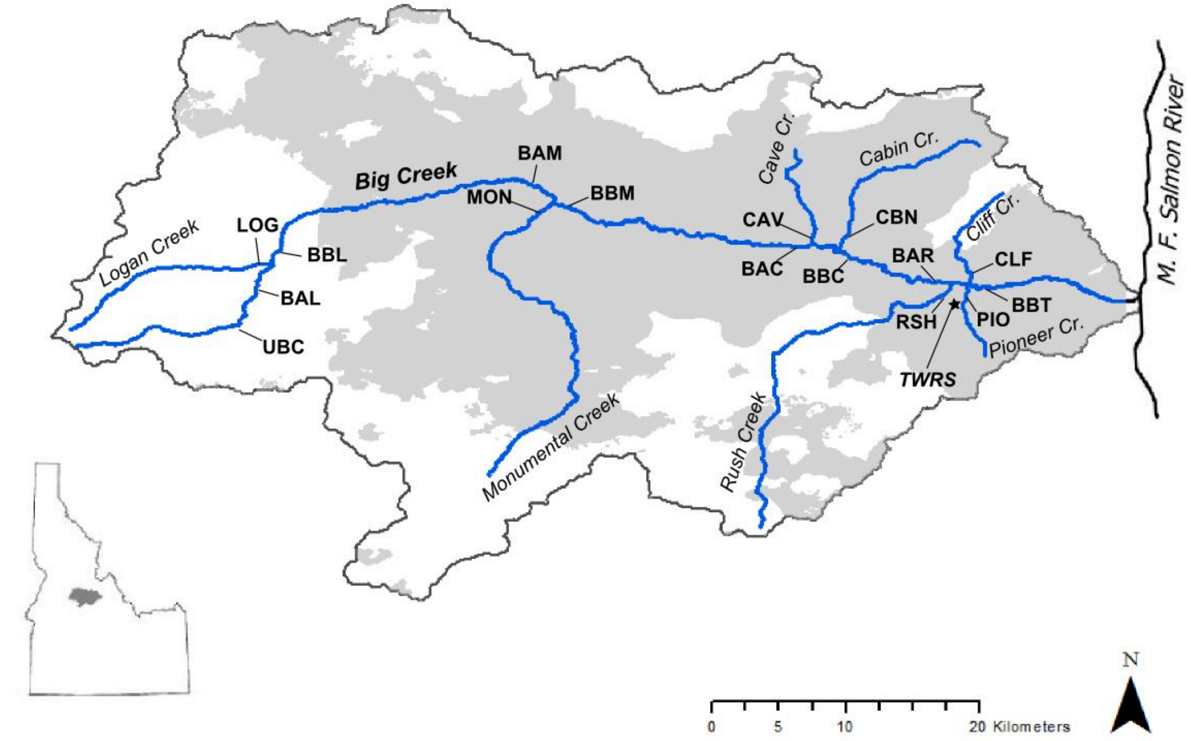


Figure 1. Map of study sites in the Big Creek watershed, Idaho, USA. Shading indicates area burned since 2000. Star indicates location of Taylor Wilderness Research Station (TWRS).

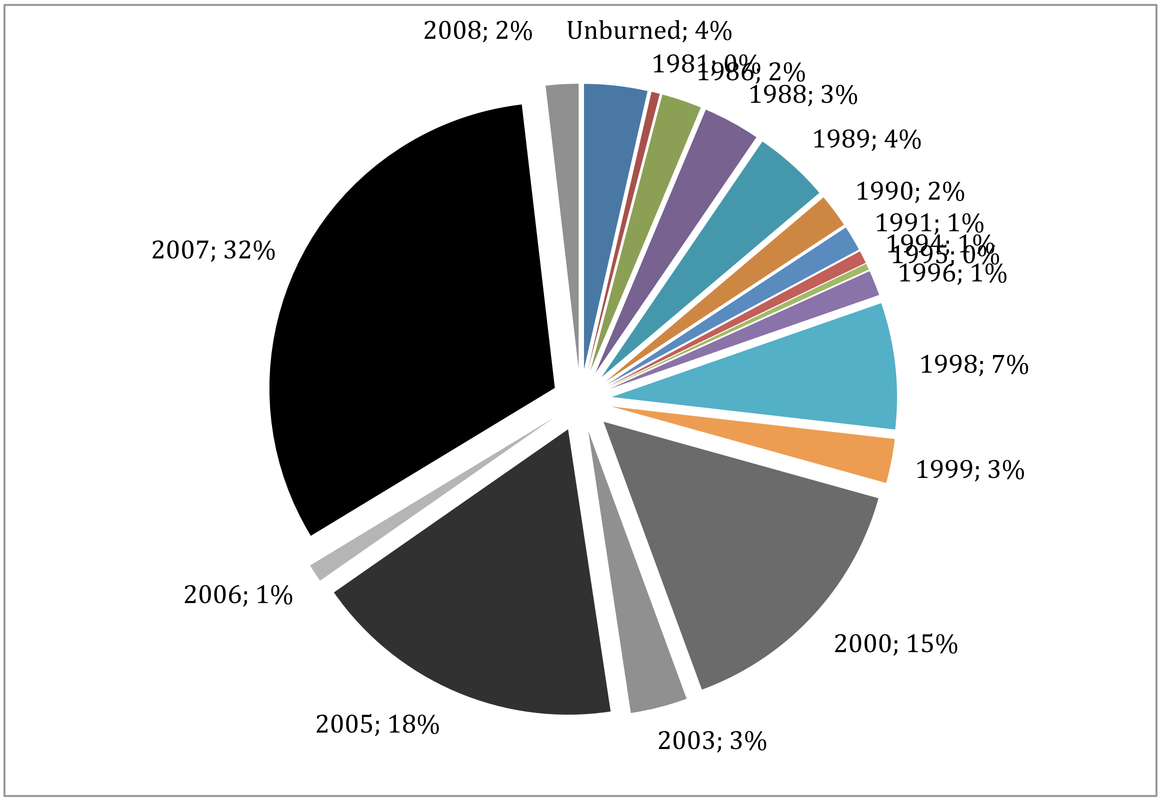


Figure 2. Overall percent of the Big Creek watershed burned, by year since 1981.

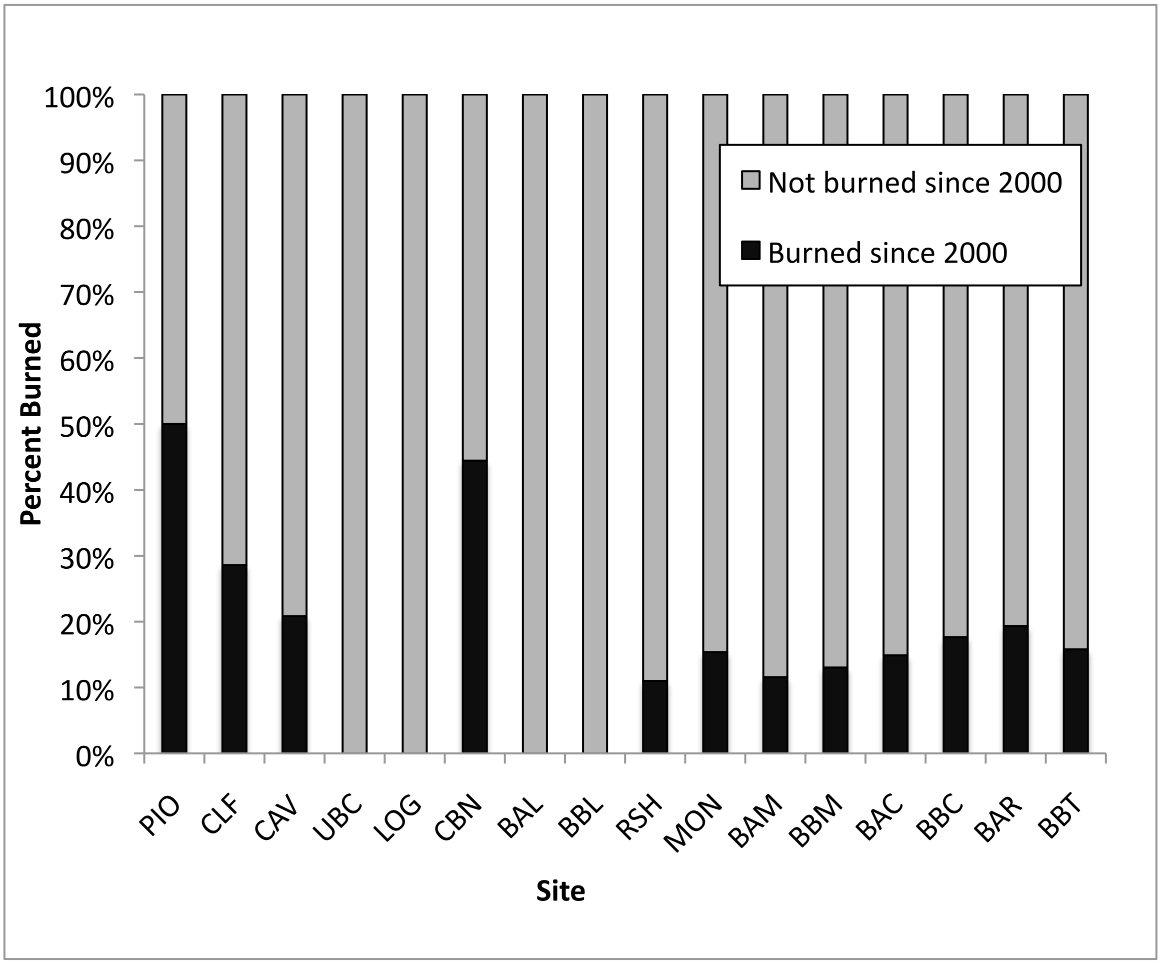


Figure 3. Percent of subbasin burned since 2000 for each site, presented from smallest drainage area to largest. Dark shading indicates area burned since 2000, light shading indicates area not burned since 2000 but does necessarily indicate unburned landscape. Developed from fire atlas data from Morgan et al. (2008).

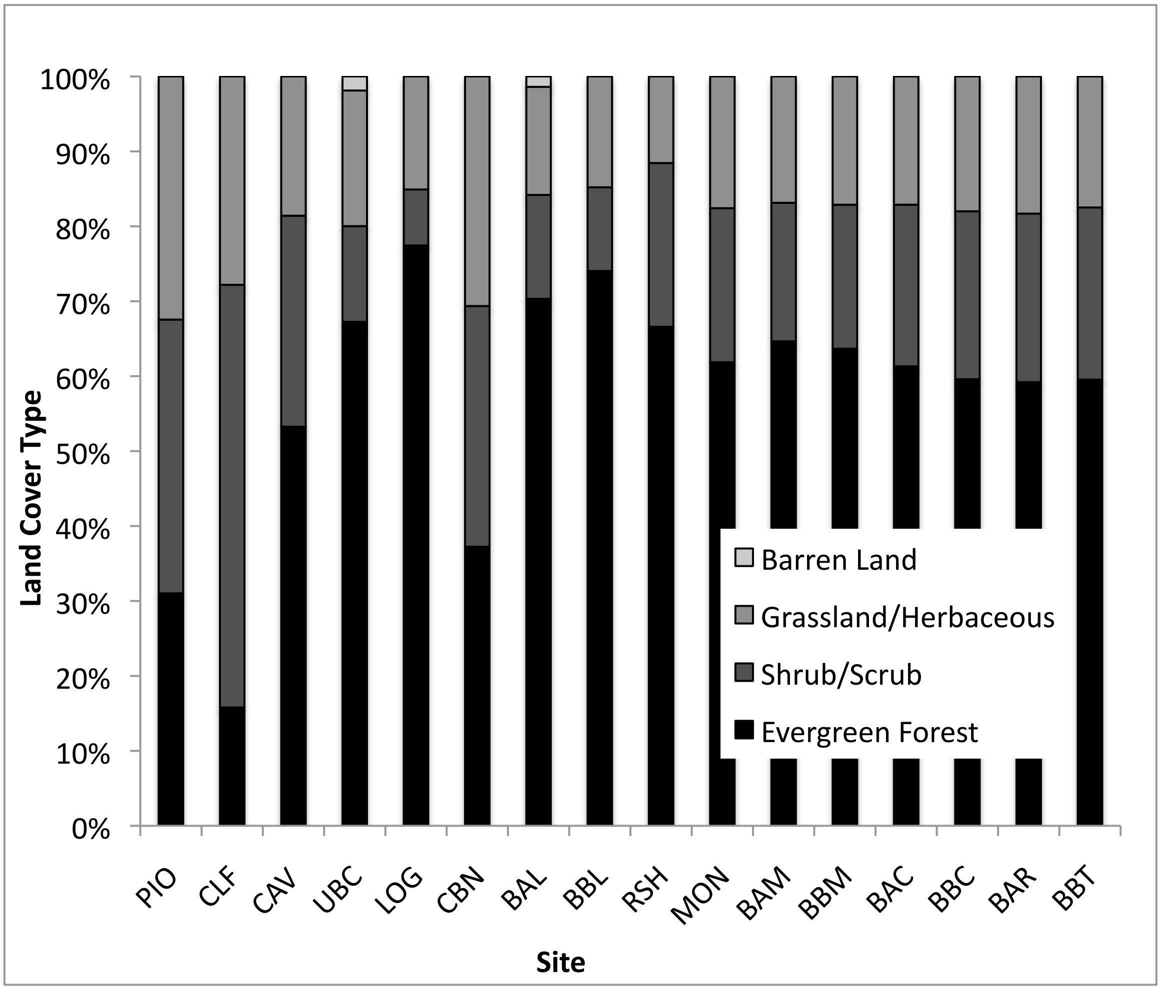


Figure 4. Dominant land cover types in the subbasin of each site, from smallest drainage area to largest, as calculated from NLCD 2006 data.

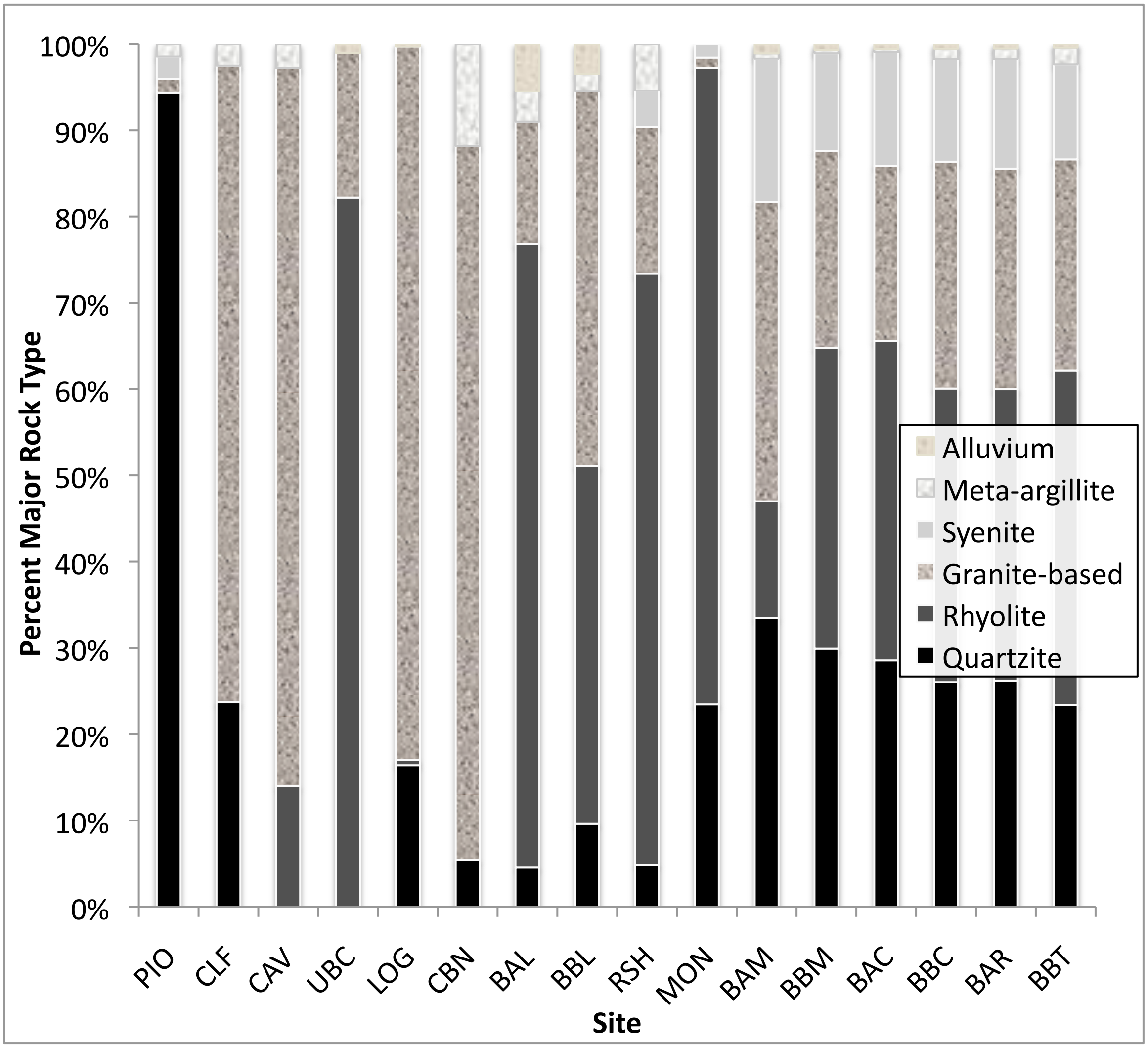


Figure 5. Percentages of major rock type found in the subbasin of each site, as calculated from Lewis and Stewart (2012).

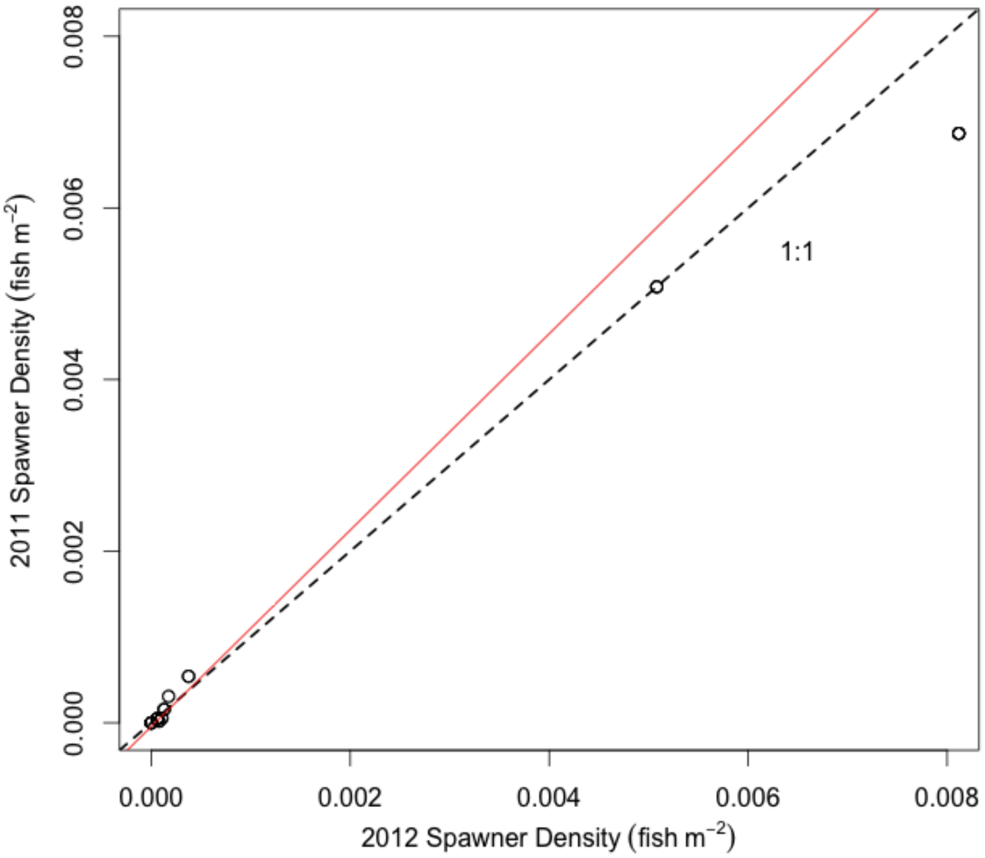


Figure 6. Adult Chinook Salmon spawner densities (fish m^{-2}) in the Big Creek watershed, Idaho, USA in 2011 and 2012, as calculated from US Forest Service aerial redd surveys (Thurow 2011, unpubl. data) with a 1.82 fish/redd expansion factor. Each point represents density calculated for stream area upstream of sampling sites according to segments used in USFS data collection, solid line represents linear regression (r^2 = 0.99), dashed line indicates 1:1 line.

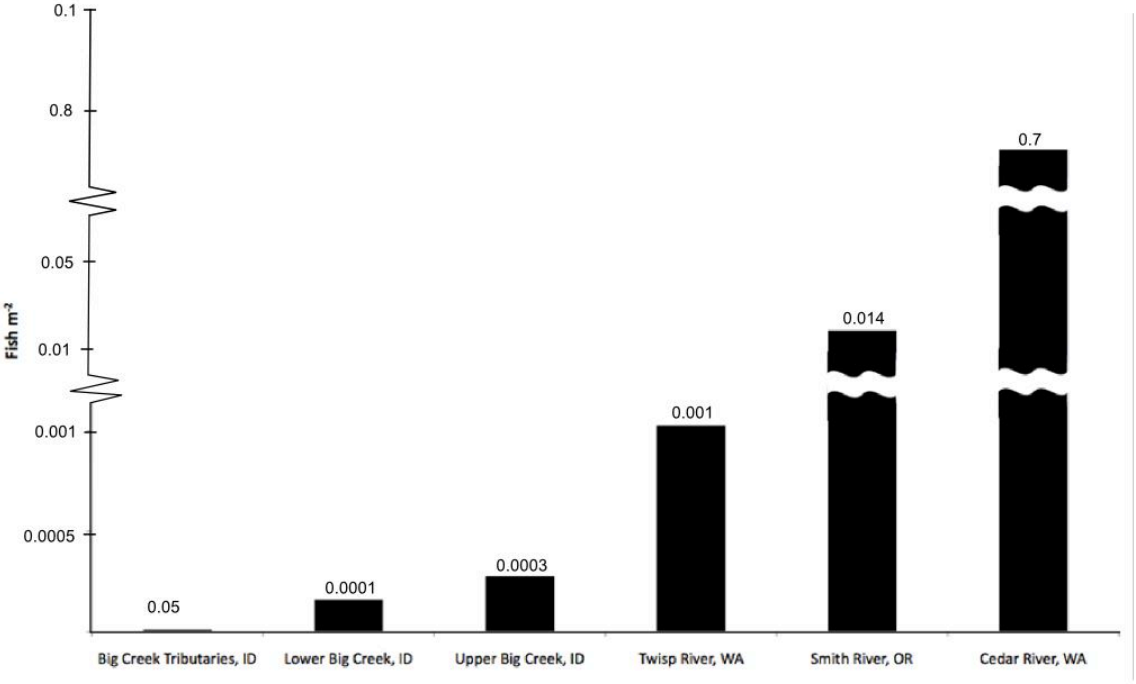


Figure 7. Comparison of salmon spawning densities in study streams and other salmon bearing streams in the Pacific Northwest (Cedar River: Cram et al. 2011, Smith River: Roni et al. 2008, Twisp River: Snow et al. 2001).

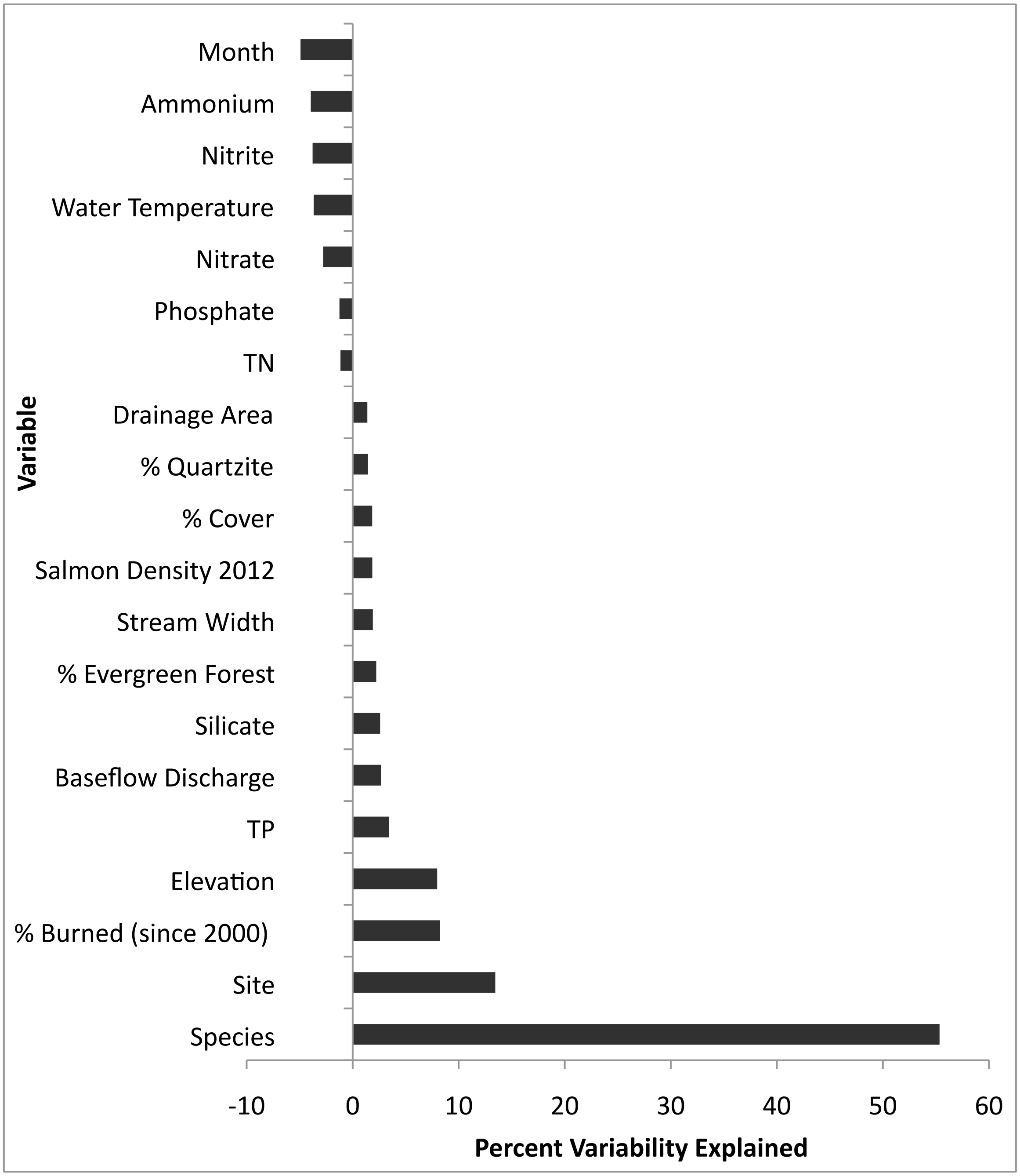


Figure 8. Variability in $\delta^{15}N$ data explained by each variable using RandomForest. Cumulative variance in nitrogen stable isotopes explained by all variables was 75%.

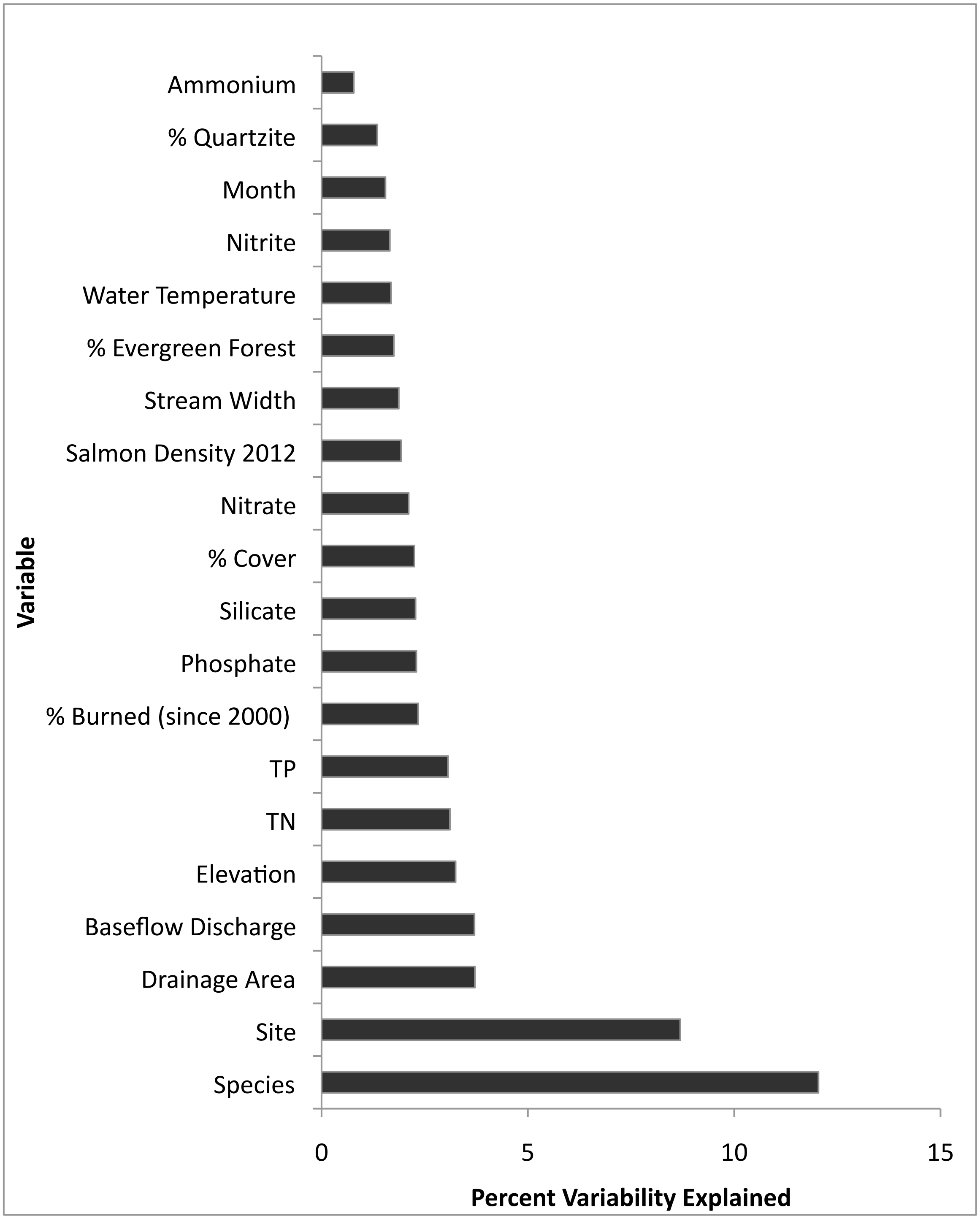


Figure 9. Variability in $\delta^{13}C$ data explained by each variable using RandomForest. Cumulative variance in carbon stable isotopes explained by all variables was 74%.

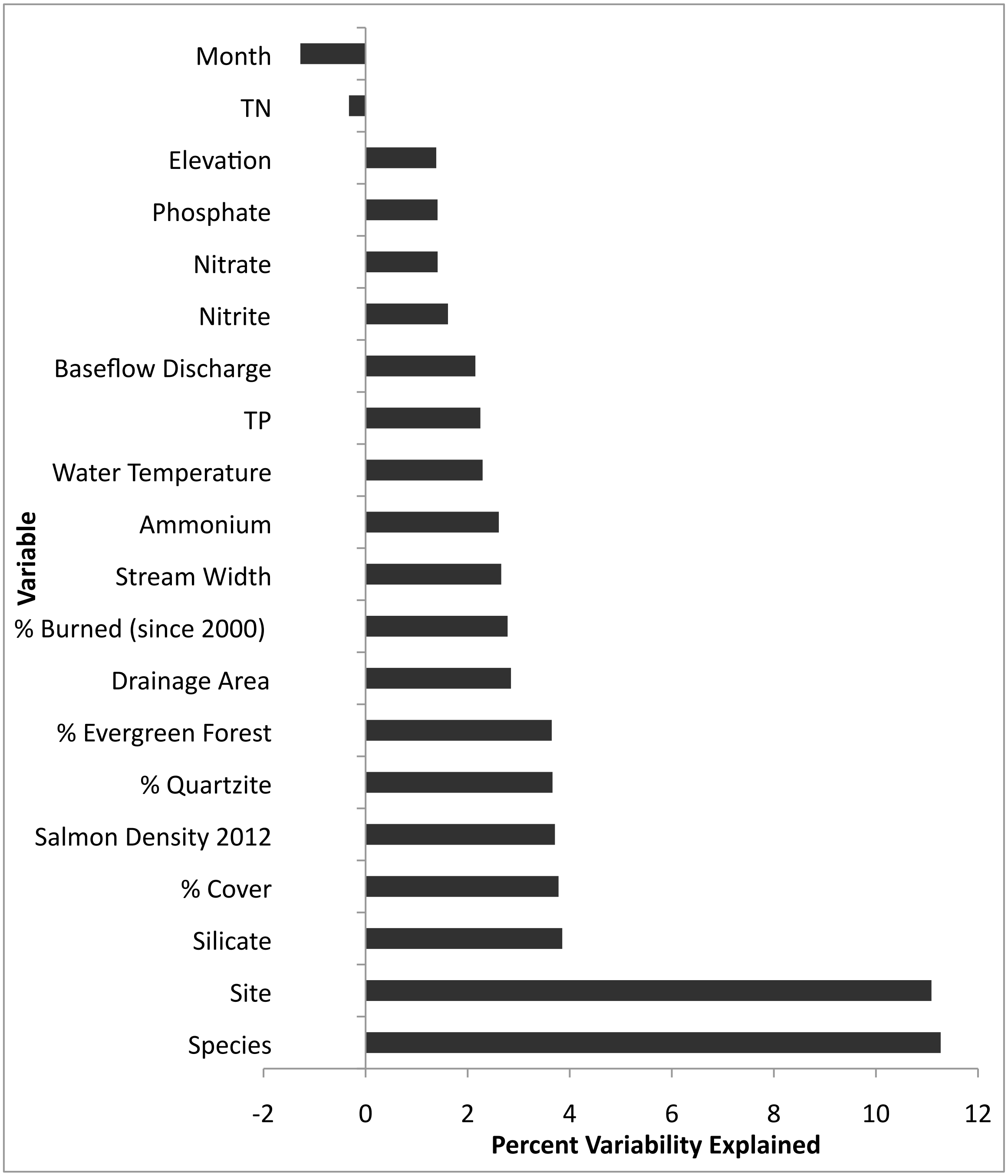


Figure 10. Variability in $\delta^{34}S$ data explained by each variable using RandomForest. Cumulative variance in sulfur stable isotopes explained by all variables was 74%.

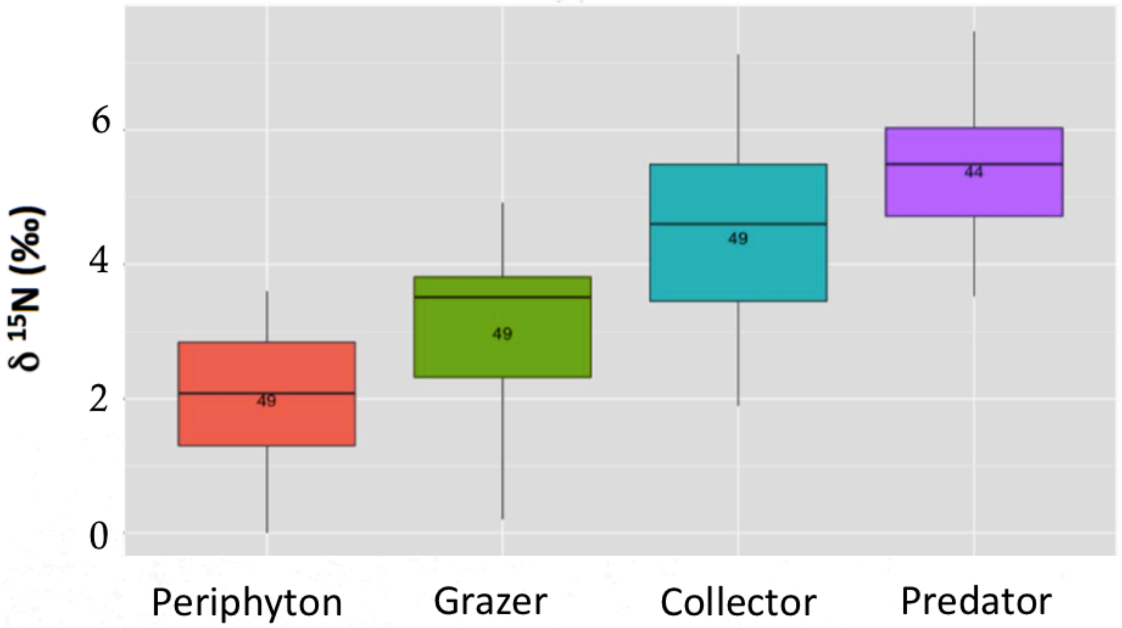


Figure 11. Observed enrichment in δ^{15}N between taxa among all sites and sampling dates in 2012. Numbers inside boxes represent number of samples for each taxa.

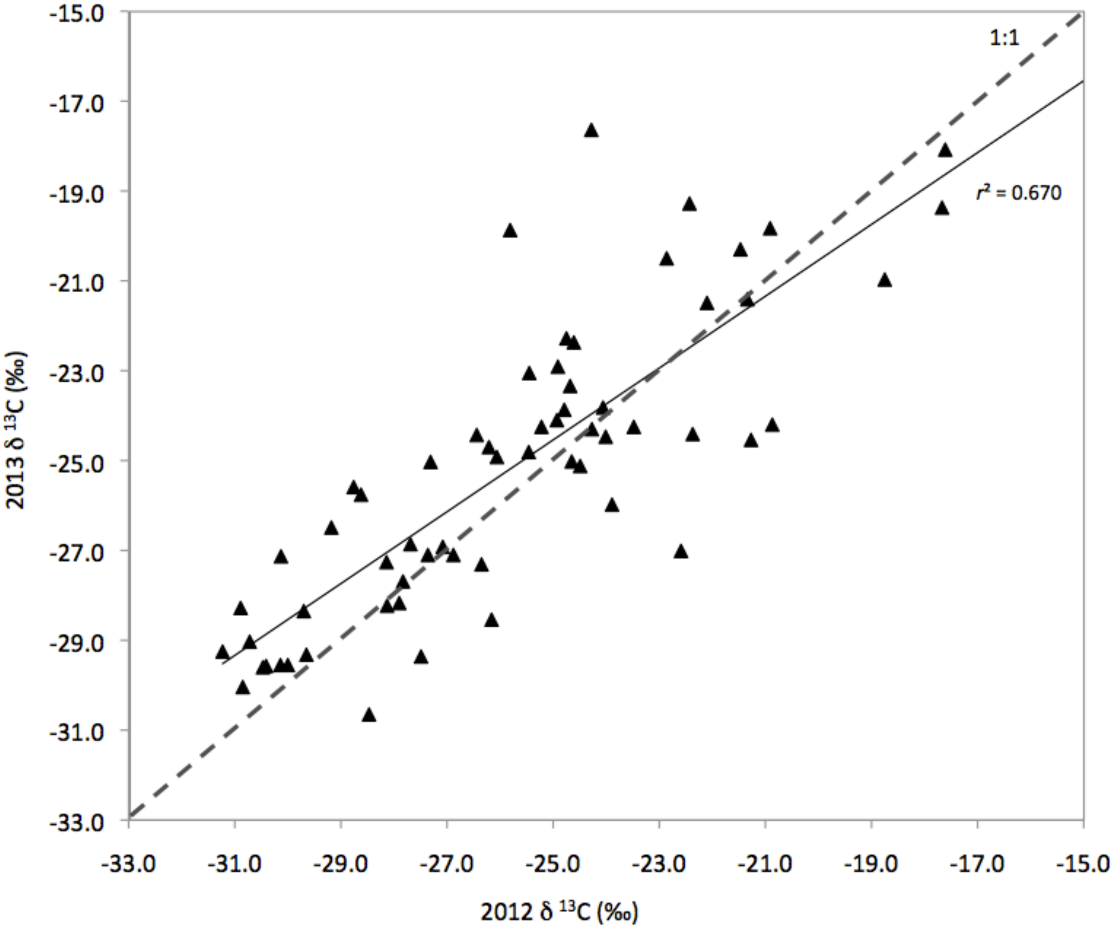


Figure 12. Interannual variability (2012-2013) in δ^{13}C values of all taxa across the Big Creek watershed, Idaho, USA.

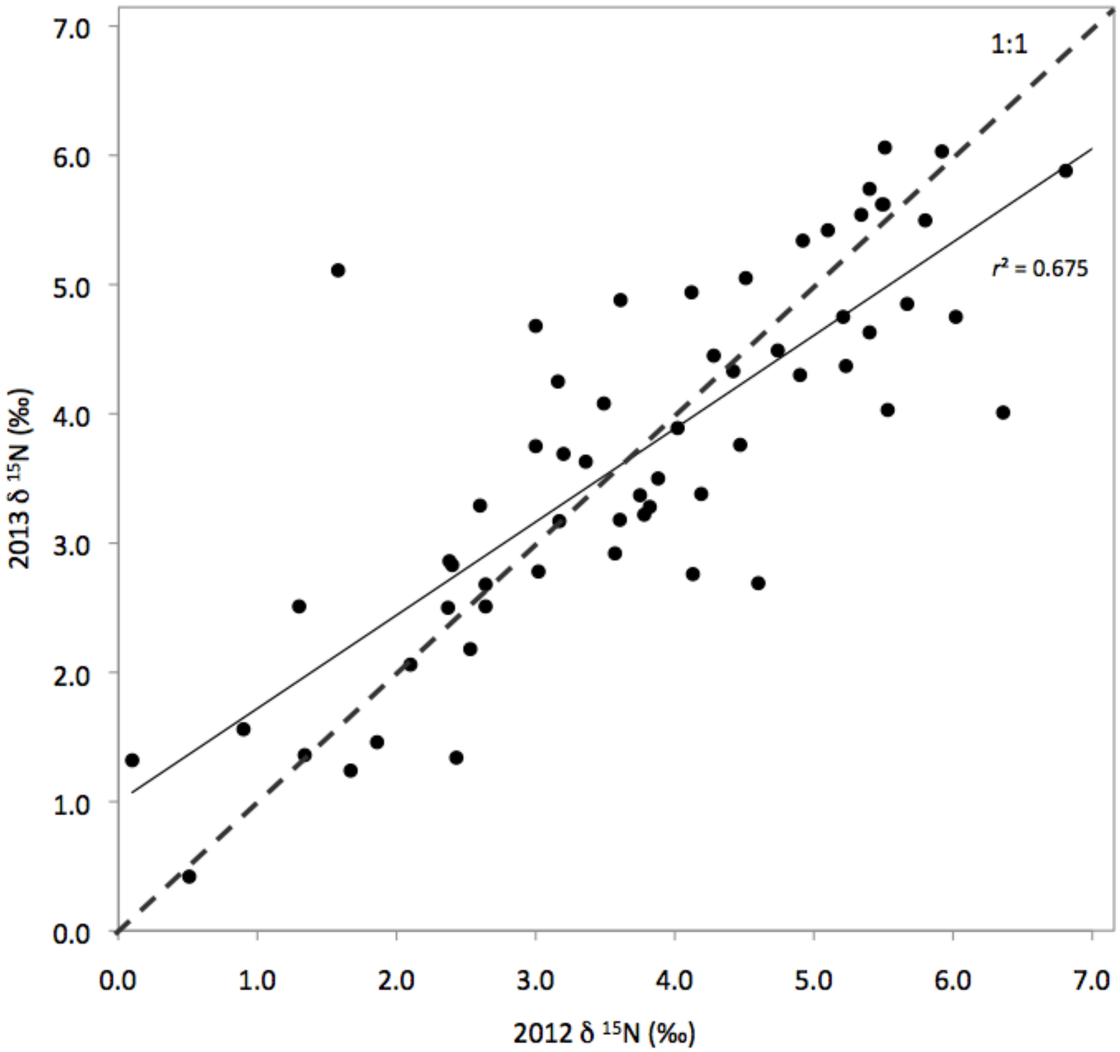


Figure 13. Interannual variability (2012-2013) in δ^{15}N values of all taxa across the Big Creek watershed, Idaho, USA.

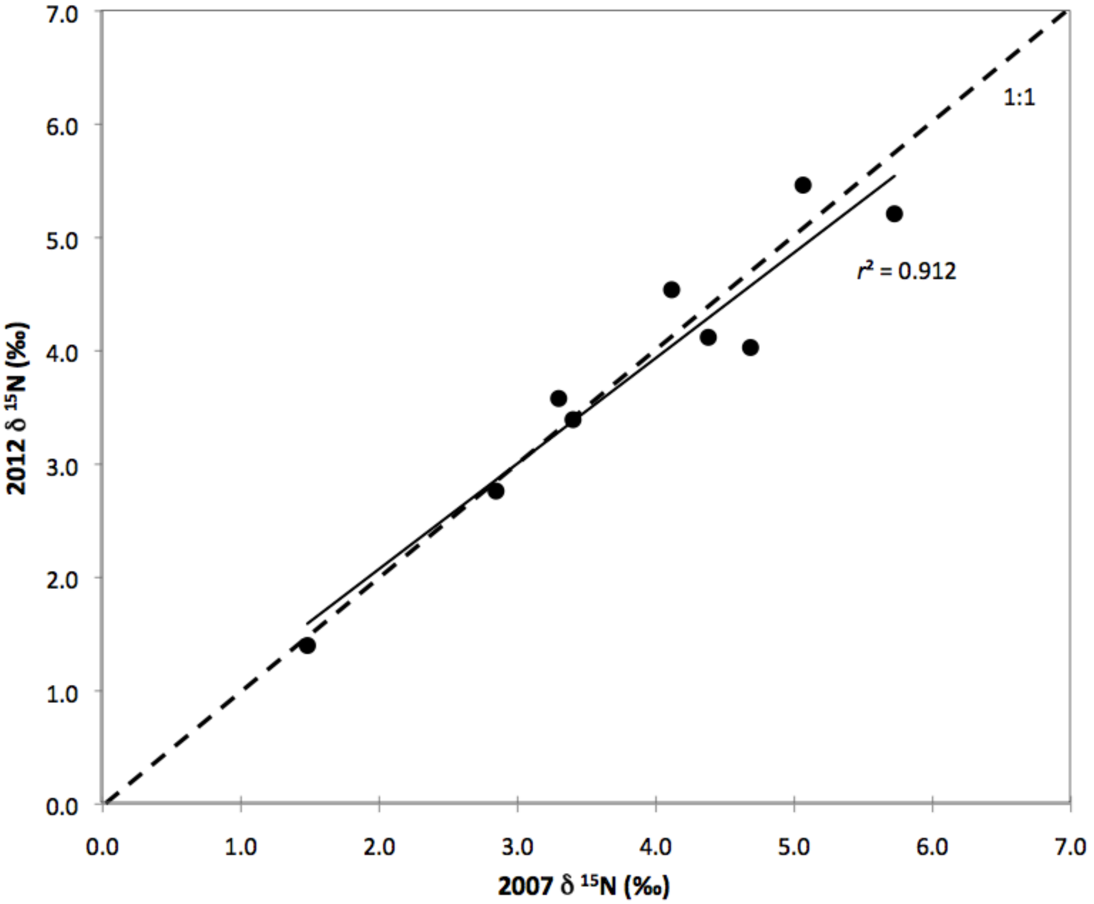


Figure 14. Interannual variability (2007-2012) in $\delta^{15}N$ values of all taxa across the Big Creek watershed, Idaho, USA.

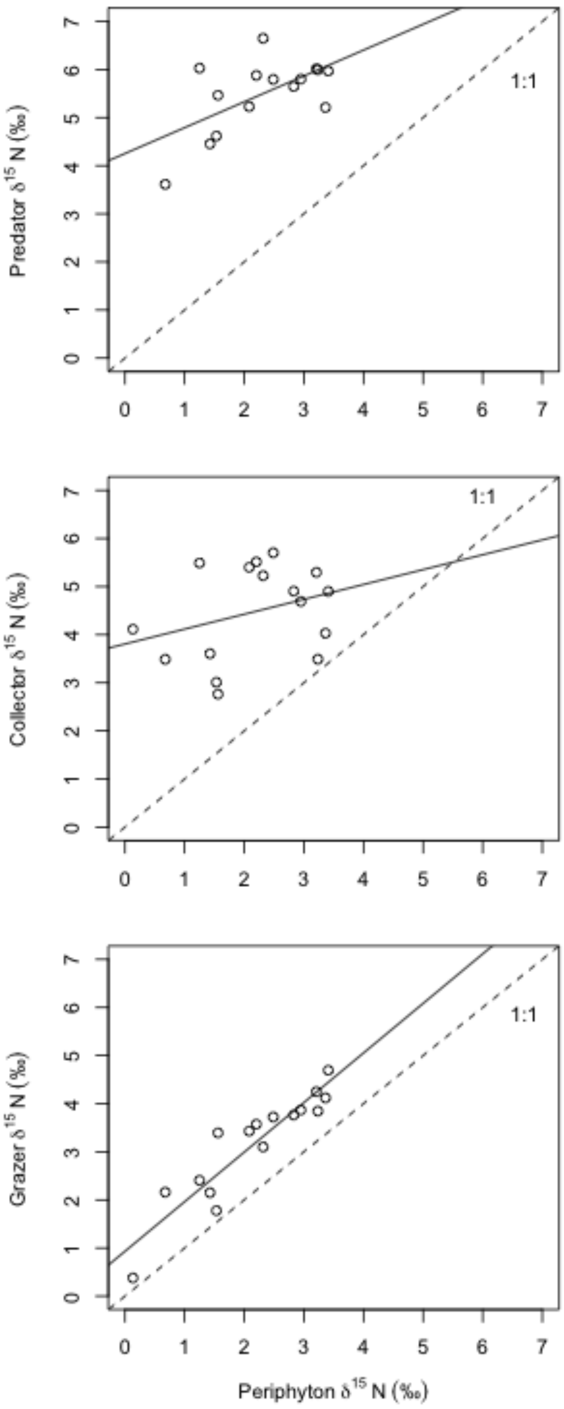


Figure 15. Relationship between the site-specific mean δ^{15}N values of periphyton versus that of grazers*, collectors, and predators*. Each point represents the mean of a site that was sampled multiple times, dashed lines indicate 1:1 line, solid lines indicate regression line, stars indicate significant relationships.

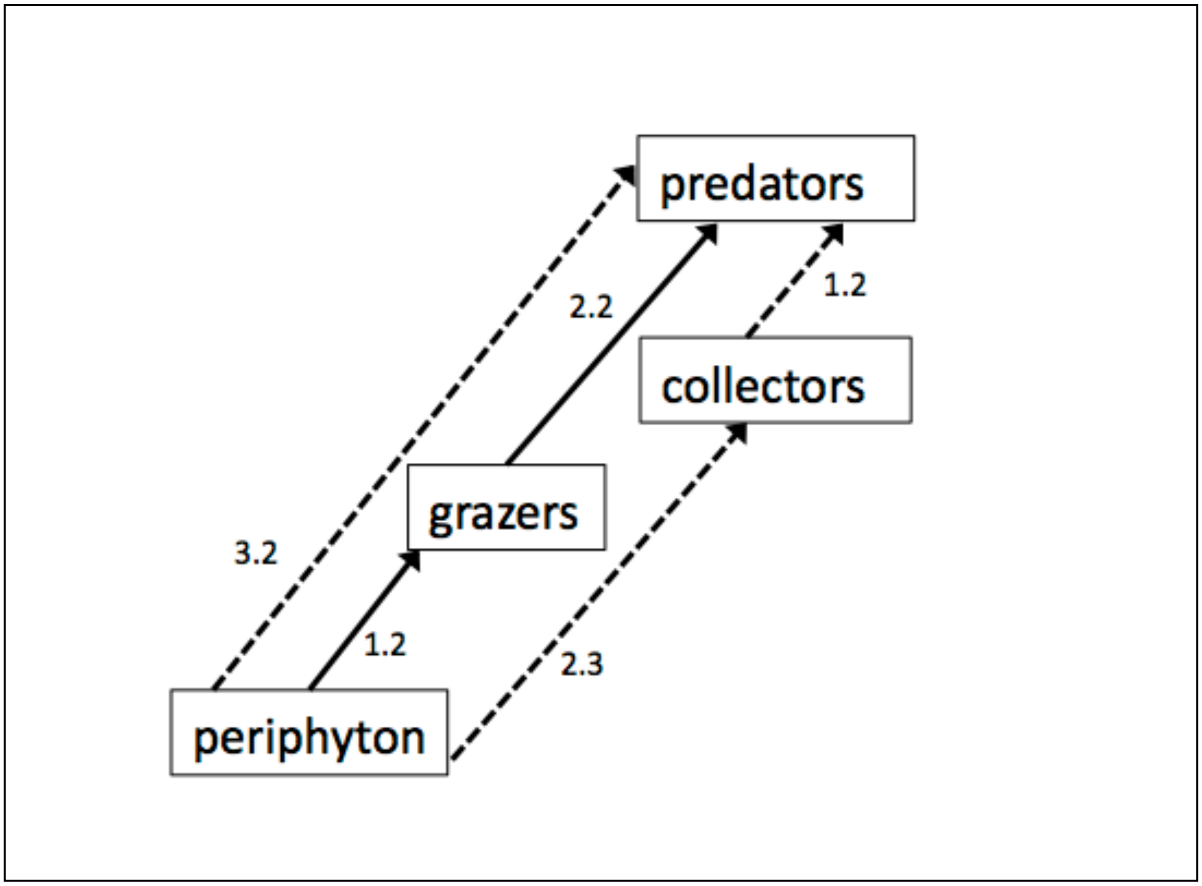


Figure 16. Conceptual diagram for estimated pathways of consumption and average values of observed discrimination $\Delta^{15}N$ (‰) for periphyton and macroinvertebrate taxa in Big Creek watershed, Idaho, USA. Grazers = *heptageniidae* mayflies, collectors = *hydropsychidae* net-spinning caddisflies, predators = *perlidae* stoneflies, periphyton = biofilm of algae and associated microbes and fungi attached to rock surfaces. Solid lines represent hypothesized direct consumption; dashed lines represent indirect consumption pathways.

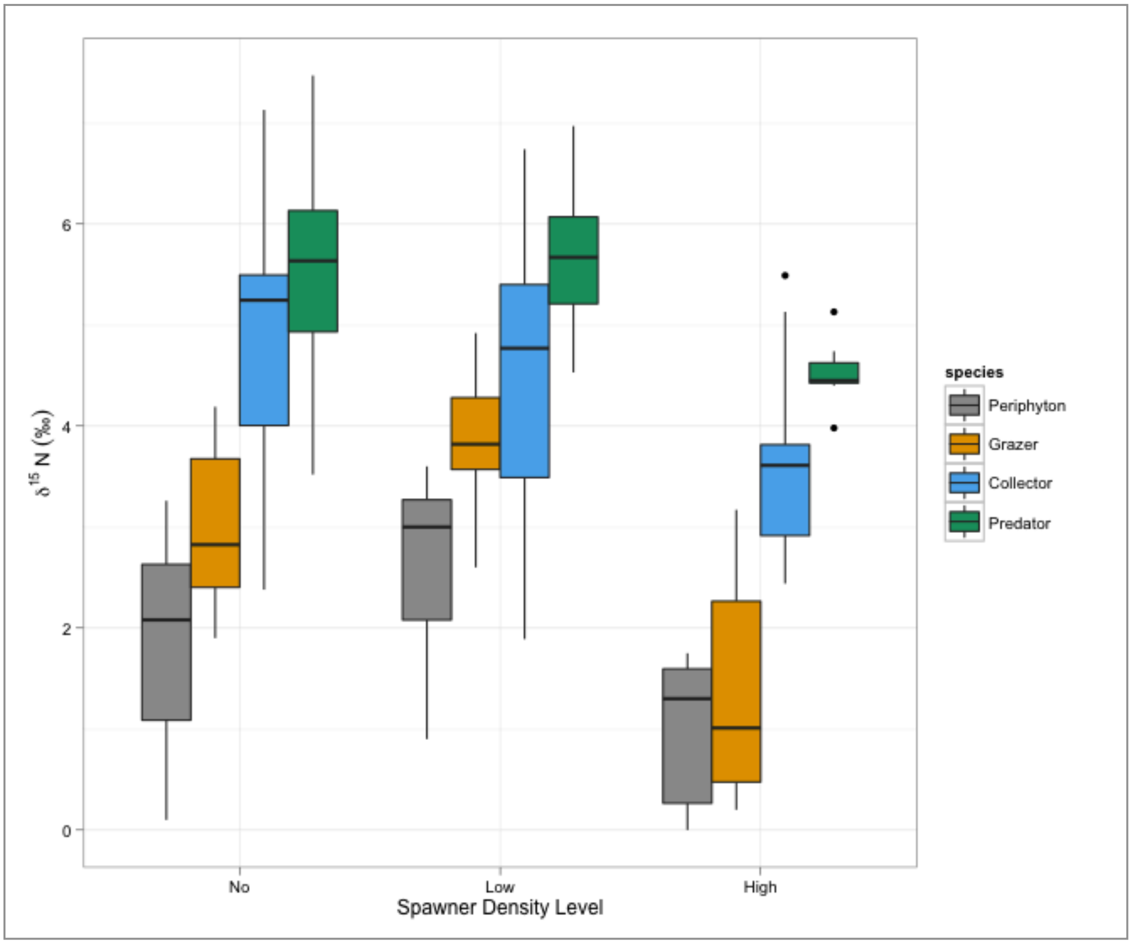


Figure 17. Nitrogen stable isotope ratios for each taxon across the entire watershed for sites with no salmon, low spawner densities (0.005—0.008 fish m^{-2}) and higher spawner densities (0.0001—$5.3x10^{-5}$ fish m^{-2}).

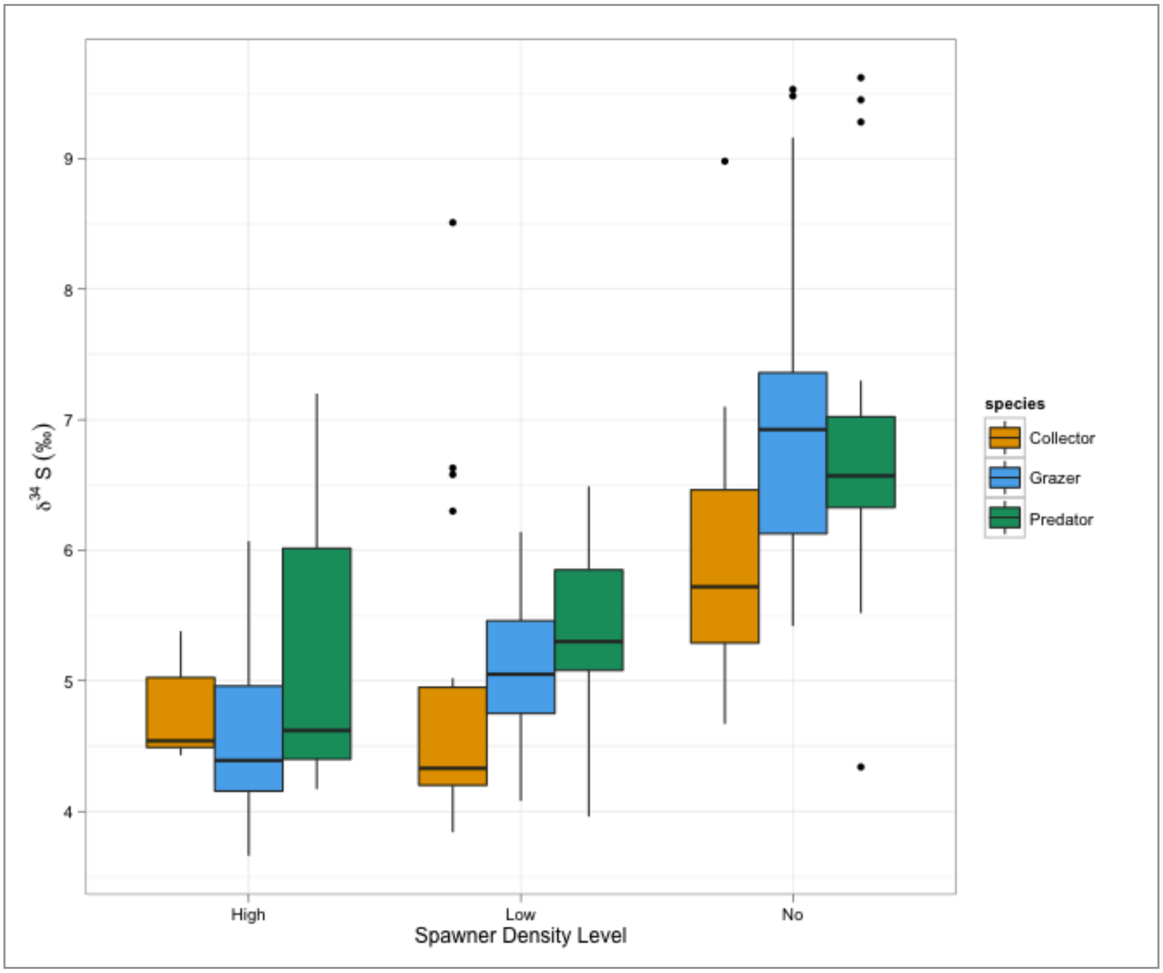


Figure 18. Sulfur stable isotope ratios for each taxon across the entire watershed for sites with no salmon, low spawner densities (0.005—0.008 fish m^{-2}) and higher spawner densities (0.0001—5.3x10^{-5} fish m^{-2}). Among all taxa, significant differences existed between salmon free sites and those with low or high spawner density.

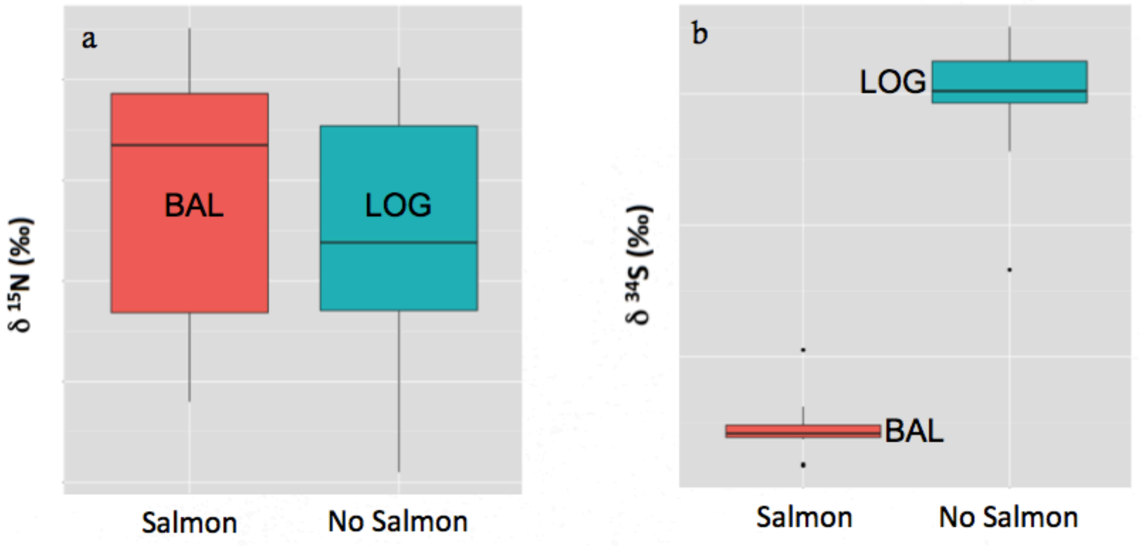


Figure 19. Local scale comparison of (a) nitrogen, (b) sulfur stable isotope ratios of pooled stream biota within the upper basin of the Big Creek watershed. Site BAL had the highest salmon spawner densities observed in the watershed, while neighboring site LOG is salmon free.

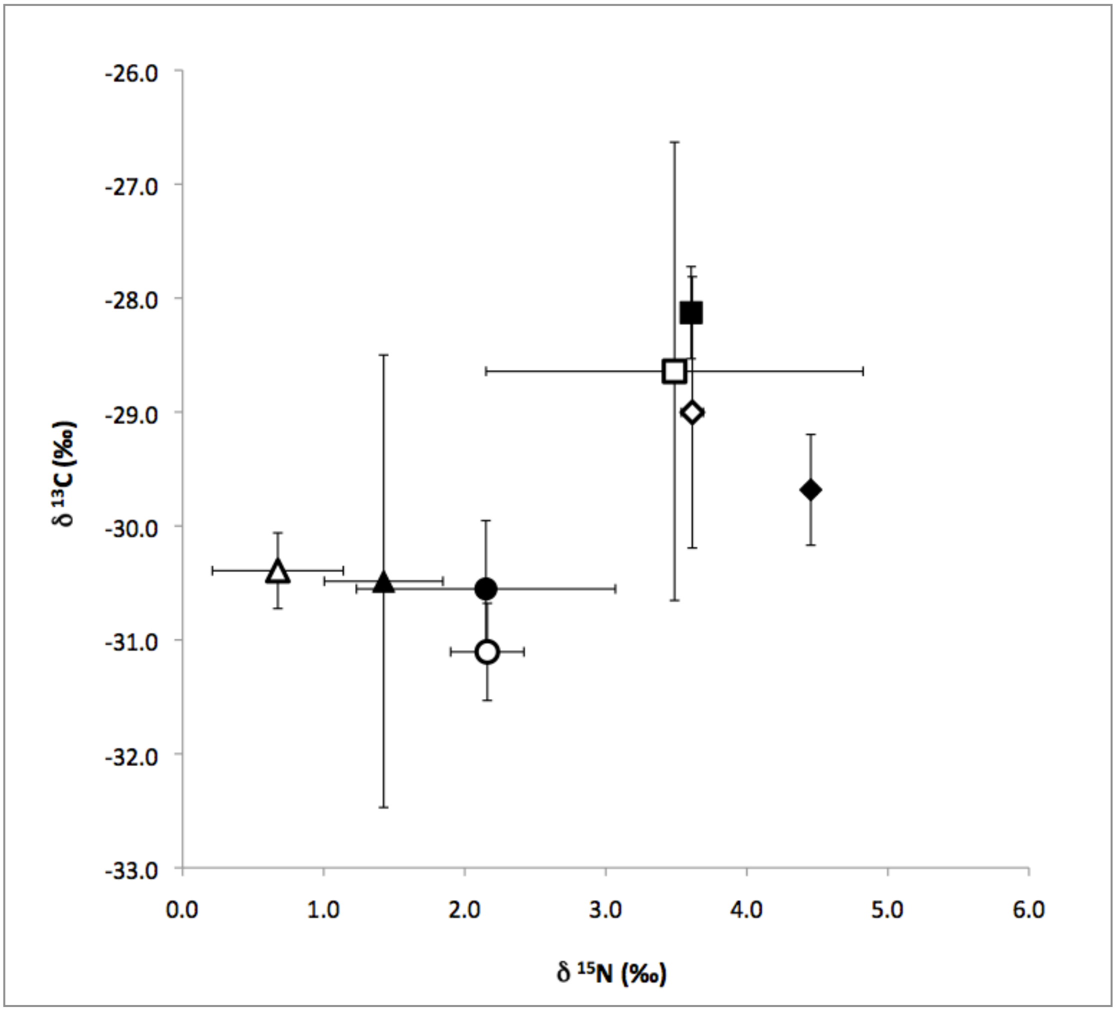


Figure 20. Dual isotope plot of in-stream biota at BAL, the highest spawning density site in upper Big Creek (filled symbols), and the salmon-free reference site LOG in Logan Creek (open symbols). Carbon stable isotopes contribute little to separation by site or taxa (triangle = periphyton, circle = grazers, square = collectors, diamond = predators). Incorporation of marine derived nutrients would shift points higher and to the right based on stable isotope composition of salmon tissues.

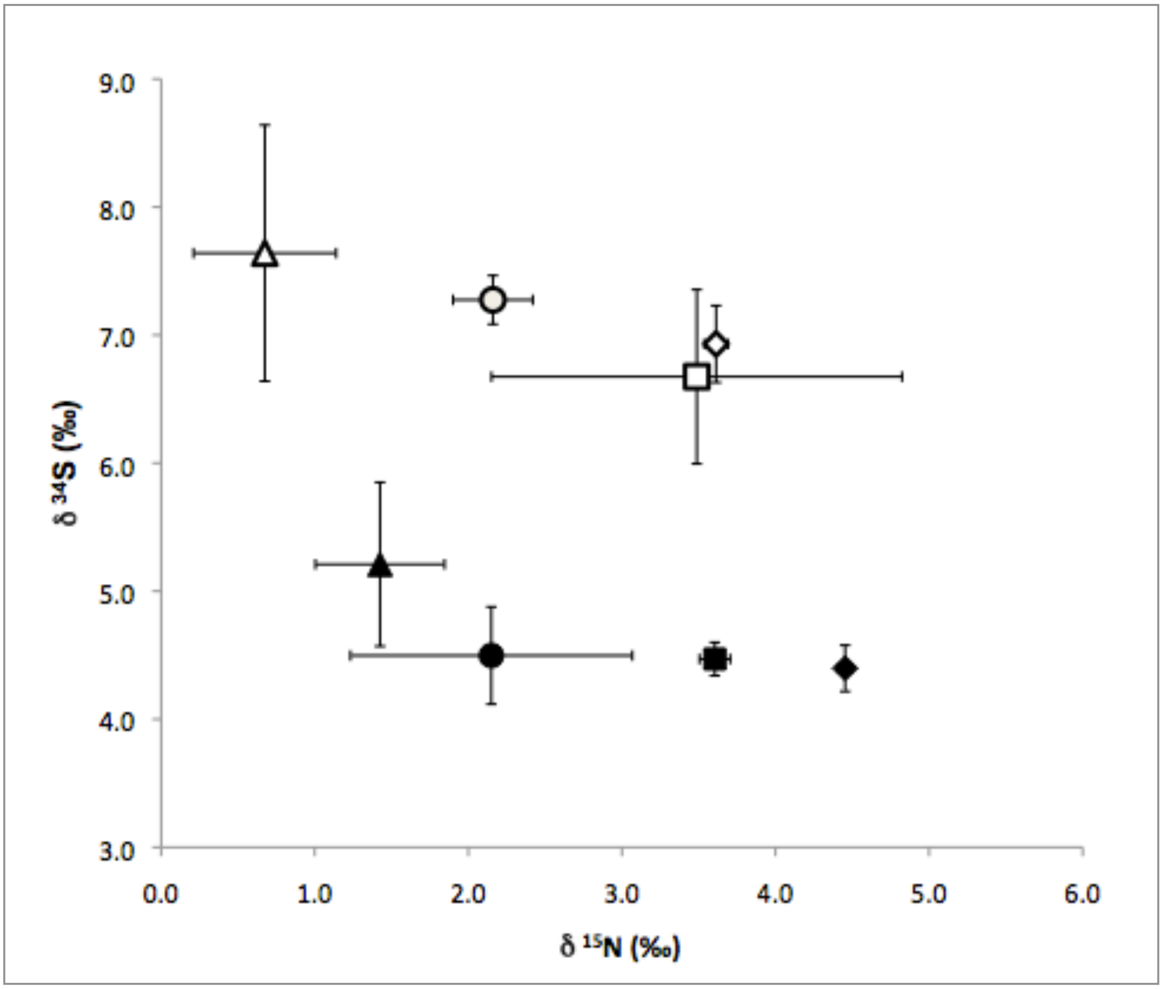


Figure 21. Dual isotope plot of in-stream biota in the salmon-bearing upper portion of Big Creek (filled symbols) and reference site in Logan Creek (open symbols). Inclusion of sulfur stable isotopes enables clear site separation, while trophic enrichment at both sites is still captured (triangle = periphyton, circle = grazers, square = collectors, diamond = predators). Incorporation of marine derived nutrients would shift points higher and to the right based on stable isotope composition of salmon tissues.

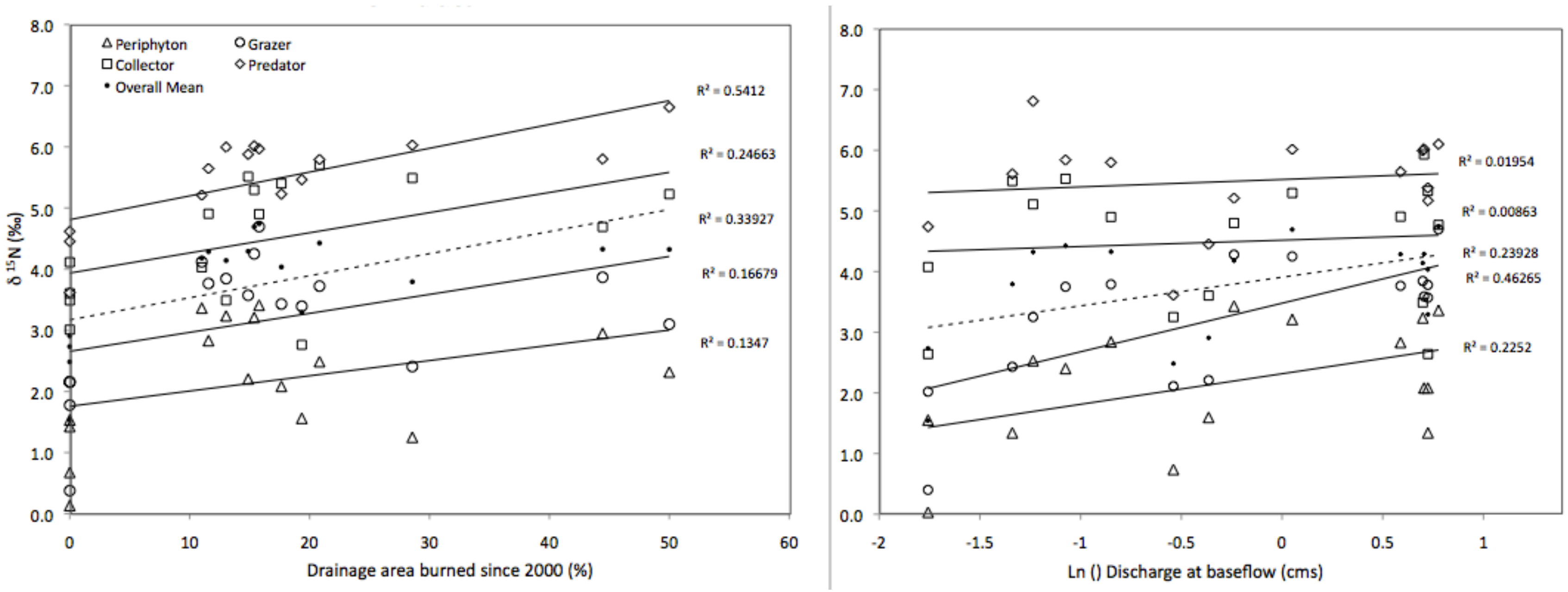


Figure 22. Nitrogen isotope ratios are positively predicted by % burn and baseflow discharge. The top model predicting each taxa contained % burn and baseflow discharge, and occasionally another less significant parameter. Dotted line represents mean among all taxa, solid lines represent regression relationship for each taxon.

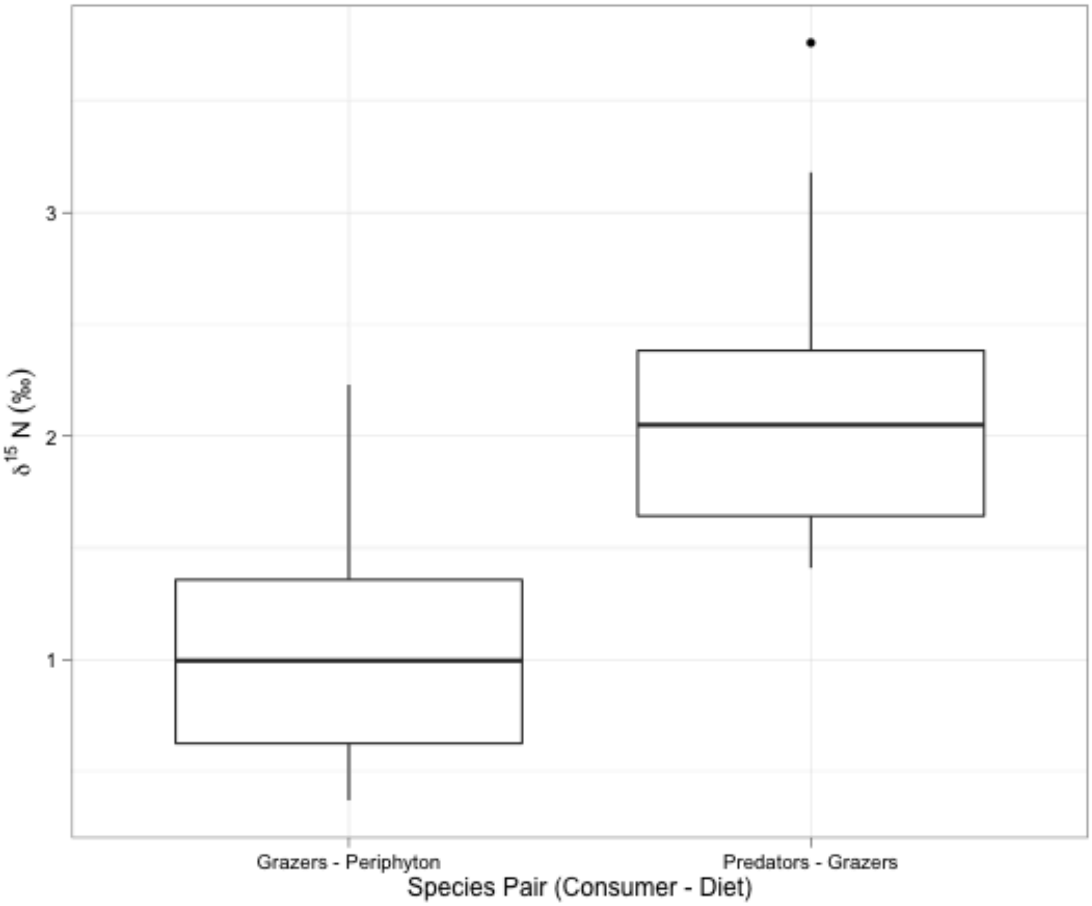
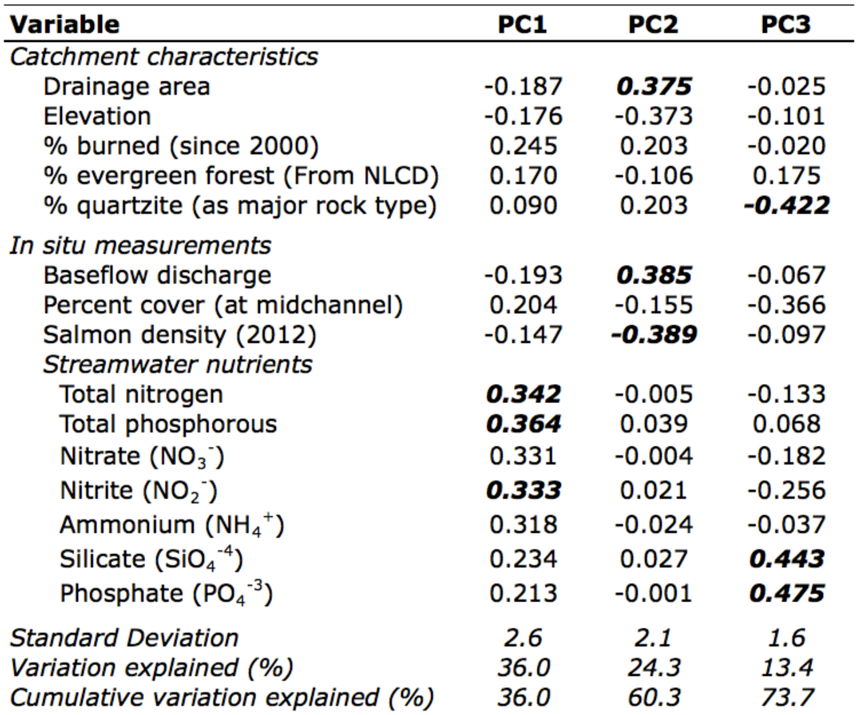


Figure 23. Observed discrimination between predicted consumer-diet pairs across the entire watershed (all sites combined).

Tables



Variable	PC1	PC2	PC3
Catchment characteristics			
Drainage area	-0.187	***0.375***	-0.025
Elevation	-0.176	-0.373	-0.101
% burned (since 2000)	0.245	0.203	-0.020
% evergreen forest (From NLCD)	0.170	-0.106	0.175
% quartzite (as major rock type)	0.090	0.203	***-0.422***
In situ measurements			
Baseflow discharge	-0.193	***0.385***	-0.067
Percent cover (at midchannel)	0.204	-0.155	-0.366
Salmon density (2012)	-0.147	***-0.389***	-0.097
Streamwater nutrients			
Total nitrogen	***0.342***	-0.005	-0.133
Total phosphorous	***0.364***	0.039	0.068
Nitrate (NO_3^-)	0.331	-0.004	-0.182
Nitrite (NO_2^-)	***0.333***	0.021	-0.256
Ammonium (NH_4^+)	0.318	-0.024	-0.037
Silicate (SiO_4^{-4})	0.234	0.027	***0.443***
Phosphate (PO_4^{-3})	0.213	-0.001	***0.475***
Standard Deviation	*2.6*	*2.1*	*1.6*
Variation explained (%)	*36.0*	*24.3*	*13.4*
Cumulative variation explained (%)	*36.0*	*60.3*	*73.7*

Table 1. Principal component analysis factor loadings for each of the original environmental variables measure. Three PC axes were included based on standard deviation > 1. Bold italics indicate the three highest loadings for each given PC axis.

Site Code	Type	UTM Easting	UTM Westing	Elevation (m)	Drainage area (km2)	% Burned (since 2000)	% Evergreen forest	% Quartzite (major rock type)	Baseflow discharge (cms)	% Cover (mid channel)	Salmon Density 2012 (fish/m2)
PIO	Small, High Burn, No Salmon	668979	4996697	1167	15.9	50.0	69.3	94.2	0.06	87.4	0
CLF	Small, High Burn, No Salmon	669159	4996760	1169	18.8	28.6	64.3	23.7	0.05	44.5	0
CAV	Small, High Burn, No Salmon	660755	4999687	1229	47.2	20.8	61.4	0.0	0.08	57.7	0
UBC	Small, Unburned, High Salmon	630729	4993363	1757	54.8	0.0	77.2	0.0	0.02	25.5	0.0051
LOG	Small, Unburned, No Salmon	632099	4997426	1745	56.2	0.0	66.5	16.4	0.29	33.8	0
CBN	Small, High Burn, No Salmon	662257	4999395	1251	64.4	44.4	63.3	5.4	0.14	3.4	0
BAL	Small, Unburned, High Salmon	632225	4997333	1696	74.7	0.0	31.0	4.5	0.43	23.1	0.0081
BBL	Small, Unburned, High Salmon	632149	4997534	1710	131.1	0.0	59.3	9.6	0.02	33.0	0.0081
RSH	Medium, Low Burn, Low Salmon	668269	4996804	1170	243.3	11.0	72.7	4.9	0.58	17.4	0.0001
MON	Medium, Low Burn Low Salmon	646928	5002449	1375	325.6	15.4	66.5	23.4	1.12	9.1	0.0002
BAM	Medium, Low Burn, Low Salmon	647002	5002708	1374	592.8	11.6	37.2	33.4	3.87	22.9	0.0001
BBM	Big, Low Burn, Low Salmon	647100	5002421	1383	918.4	13.0	59.3	29.9	5.00	1.9	0.0001
BAC	Big, Low Burn, Low Salmon	660720	4999643	1274	1037.0	14.9	15.8	28.5	5.07	15.9	0.0001
BBC	Big, Low Burn, Low Salmon	662757	4998605	1209	1151.2	17.7	58.9	26.0	5.29	1.8	0.0004
BAR	Big, Low Burn, Low Salmon	668269	4996804	1170	1184.3	19.4	53.0	26.1	5.30	0.0	0.0001
BBT	Big, Low Burn, Low Salmon	669380	4996597	1160	1463.2	15.8	61.0	23.3	5.98	12.2	0.0001

Table 2. Physical and environmental characteristics of sampling sites and associated subbasins, listed by increasing drainage area, for all sampling sites in Big Creek watershed, Idaho, USA.

	$\delta^{15}N$						$\delta^{13}C$						$\delta^{34}S$					
Source of Variation	df	Sum of Squares	Mean Square	F	*p*	Sig. Level	df	Sum of Squares	Mean Square	F	*p*	Sig. Level	df	Sum of Squares	Mean Square	F	*p*	Sig. Level
Periphyton																		
Site	15	47.96	3.20	48.72	0.0009	***	15	379.10	25.28	77.87	0.0004	***						
Month	2	0.73	0.37	5.57	0.0698		2	14.50	7.23	22.29	0.0068	**			N/A			
Site **x** Month	26	3.63	0.14	2.13	0.2430		26	78.30	3.01	9.28	0.0212	*						
Residuals	4	0.26	0.07				4	1.30	0.33									
Collector																		
Site	15	42.60	2.84	2.50	0.1950		15	312.11	20.81	47.59	0.0010	***	15	36.81	2.45	83.26	0.0003	***
Month	2	1.53	0.76	0.67	0.5610		2	20.44	10.22	23.37	0.0062	**	2	0.18	0.09	3.02	0.1588	
Site **x** Month	26	33.29	1.28	1.13	0.5150		26	62.20	2.39	5.47	0.0547		26	24.71	0.95	32.25	0.0020	**
Residuals	4	4.55	1.14				4	1.75	0.44				4	0.12	0.03			
Grazer																		
Site	15	62.72	4.18	69.63	0.0005	***	15	276.01	18.40	15.96	0.0080	**	15	85.91	5.73	76.91	0.0004	***
Month	2	0.96	0.48	8.01	0.0399	*	2	19.10	9.55	8.28	0.0378	*	2	0.36	0.18	2.44	0.2027	
Site **x** Month	26	6.50	0.25	4.16	0.0871		26	26.41	1.02	0.88	0.6381		26	3.10	0.12	1.60	0.3504	
Residuals	4	0.24	0.06				4	4.61	1.15				4	0.30	0.07			
Predator																		
Site	14	27.68	1.98	71.58	0.0024	**	14	257.95	18.43	14.08	0.0255	*	14	64.46	4.60	57.93	0.0032	**
Month	2	0.85	0.42	15.34	0.0266	*	2	2.41	1.21	0.92	0.4874		2	0.12	0.06	0.76	0.5406	
Site **x** Month	23	6.82	0.30	10.73	0.0369	*	23	31.75	1.38	1.06	0.5661		23	7.45	0.32	4.08	0.1361	
Residuals	3	0.08	0.03				3	3.93	1.31				3	0.24	0.08			

Table 3. Results of the analysis of variance (two-way ANOVA with interaction) of nitrogen, carbon and sulfur isotopic ratios for each taxon. Stars indicate significance level at $\alpha = 0.05$.

Source of Variation	df	Sum of Squares	Mean Square	F	*p*	Sig. Level
δ^{15}N						
Species	3	309.81	103.27	301.49	< 0.0000	***
Site	15	127.54	8.50	24.82	< 0.0000	***
Month	2	2.52	1.26	3.68	0.0503	
Species x Site	44	54.16	1.23	3.59	0.0047	**
Species x Month	6	2.24	0.37	1.09	0.4128	
Site x Month	26	15.13	0.58	1.70	0.1427	
Species x Site x Month	76	36.21	0.48	1.39	0.2419	
Residuals	15	5.14	0.34			
δ^{13}C						
Species	3	1087.90	72.53	93.92	< 0.0000	***
Site	15	31.40	15.68	20.31	0.0001	***
Month	2	280.40	93.46	121.03	< 0.0000	***
Species x Site	44	95.90	3.69	4.78	0.0014	**
Species x Month	6	146.30	3.32	4.31	0.0018	**
Site x Month	26	26.00	4.33	5.60	0.0032	**
Species x Site x Month	76	103.80	1.37	1.77	0.1077	
Residuals	15	11.60	0.77			
δ^{34}S						
Species	2	182.46	12.16	17.29	< 0.0000	***
Site	15	0.71	0.35	0.50	0.6150	
Month	2	31.79	10.60	15.06	0.0001	***
Species x Site	29	17.33	0.67	0.95	0.5630	
Species x Month	4	42.29	0.96	1.37	0.2600	
Site x Month	26	3.29	0.55	0.78	0.5990	
Species x Site x Month	75	63.46	0.84	1.19	0.3720	
Residuals	15	10.55	0.70			

Table 4. Results of the analysis of variance (Three-way ANOVA with interaction) of nitrogen, carbon and sulfur isotopic ratios by taxa (4 levels), site (16 levels) and month (3 levels). Stars indicate significance level at $\alpha = 0.05$.

	δ¹⁵N														
	Periphyton			Grazer			Collector			Predator			All Taxa Combined		
Site	Mean	(SD)	Range	Mean	(SD)	Range	Mean	(SD)	Range	Mean	(SD)	Range	Mean	(SD)	Range
BAC	2.2	0.4	0.8	3.6	0.3	0.5	5.5	0.8	1.4	5.9	1.2	2.3	4.3	0.7	1.3
BAL	1.4	0.4	0.9	2.2	0.9	2.2	3.6	0.1	0.2	4.5	0.0	0.1	2.9	0.4	0.8
BAM	2.8	0.2	0.3	3.8	0.4	0.5	4.9	2.1	2.9	5.6	0.2	0.3	4.3	0.7	1.0
BAR	1.6	0.8	1.5	3.4	0.3	0.6	2.8	0.5	0.9	5.5	0.6	1.0	3.3	0.5	1.0
BBC	2.1	0.4	0.8	3.4	0.7	1.3	5.4	1.3	2.6	5.2	0.3	0.5	4.0	0.7	1.3
BBL	1.5	0.2	0.5	1.8	1.0	2.0	3.0	0.8	1.5	4.6	0.6	1.2	2.7	0.7	1.3
BBM	3.2	0.3	0.5	3.8	0.0	0.1	3.5	0.0	0.0	6.0	0.1	0.2	4.1	0.1	0.2
BBT	3.4	0.2	0.3	4.7	0.2	0.5	4.9	0.9	1.7	6.0	0.5	1.0	4.7	0.4	0.9
CAV	2.5	0.2	0.4	3.7	0.1	0.1	5.7	0.4	0.8	5.8	0.4	0.9	4.4	0.3	0.5
CBN	3.0	0.3	0.5	3.9	0.3	0.6	4.7	0.9	1.9	5.8	0.3	0.6	4.3	0.5	0.9
CLF	1.3	0.4	0.8	2.4	0.1	0.2	5.5	0.0	0.0	6.0	0.8	1.5	3.8	0.3	0.6
LOG	0.7	0.5	1.0	2.2	0.3	0.6	3.5	1.3	2.7	3.6	0.1	0.0	2.5	0.5	1.1
MON	3.2	0.0	0.0	4.3	0.2	0.3	5.3	0.1	0.1	6.0	0.5	0.7	4.7	0.2	0.3
PIO	2.3	0.4	0.8	3.1	0.5	1.1	5.2	1.8	3.7	6.6	0.9	1.8	4.3	0.9	1.8
RSH	3.4	0.2	0.3	4.1	0.5	0.9	4.0	1.9	3.5	5.2	0.7	1.4	4.2	0.8	1.5
UBC	0.1	0.2	0.5	0.4	0.1	0.3	4.1	1.4	2.7	--	--	--	1.5	0.6	1.2
All Sites	2.2	1.0	3.6	3.2	1.1	4.7	4.5	1.0	5.2	5.5	0.8	3.9	3.9	0.7	1.0

Table 5. Summary of $\delta^{15}N$ values for all taxa across all sites.

Model	R^2	F	df	p	k	AICc	ΔAIC	Model Likelihood	w_i
Periphyton									
Baseflow discharge + % Burned + TN	0.30	7.82	3,44	0.0003	5	131.50	0.00	1.000	0.607
Baseflow discharge + % Burned	0.28	10.09	2,45	0.0002	4	131.74	0.24	0.887	0.539
Baseflow discharge + % Burned + TN +%Qtz + %Cover	0.30	4.99	5,42	0.0011	7	135.03	3.53	0.171	0.104
% Burned	0.16	10.05	1,46	0.0027	3	137.65	6.15	0.046	0.028
Baseflow discharge	0.11	6.84	1,46	0.0120	3	140.48	8.98	0.011	0.007
Grazer									
Baseflow discharge + % Burned + %Qtz	0.44	13.24	3,44	< 0.0001	5	135.18	0.00	1.000	0.607
Baseflow discharge + % Burned	0.42	17.86	2,45	< 0.0001	4	135.51	0.33	0.848	0.515
Baseflow discharge + % Burned + TN	0.42	12.52	3,44	< 0.0001	5	136.43	1.25	0.535	0.325
Baseflow discharge + % Burned + TN +%Qtz + %Cover	0.43	8.09	5,42	< 0.0001	7	139.05	3.87	0.144	0.088
Baseflow discharge	0.23	14.93	1,46	0.0003	3	147.68	12.50	0.002	0.001
% Burned	0.18	11.25	1,46	0.0016	3	150.67	15.49	0.000	0.000
Collector									
Baseflow discharge + % Burned	0.17	10.42	2,93	< 0.0001	4	331.97	0.00	1.000	0.607
Baseflow discharge + % Burned + %Qtz	0.17	7.32	3,92	0.0002	5	333.05	1.08	0.583	0.354
Baseflow discharge + % Burned + TN +%Qtz + %Cover	0.17	4.76	5,90	0.0007	7	335.67	3.70	0.157	0.095
% Burned	0.12	13.90	1,94	0.0003	3	335.96	3.99	0.136	0.083
Baseflow discharge	0.04	5.35	1,94	0.0230	3	343.89	11.92	0.003	0.002
Predator									
Baseflow discharge + % Burned	0.50	22.37	2,41	<0.0001	4	94.90	0.00	1.000	0.607
Baseflow discharge + % Burned + TN	0.50	15.26	3,40	<0.0001	5	96.40	1.50	0.472	0.287
% Burned	0.43	33.45	1,43	<0.0002	3	99.20	4.30	0.116	0.071
Baseflow discharge + % Burned + TN +%Qtz + %Cover	0.49	9.20	5,38	< 0.0001	7	100.60	5.70	0.058	0.035
Baseflow discharge	0.03	2.18	1,42	0.1470	3	122.76	27.86	0.000	0.000

Table 6. Results of model selection using AICc for multiple linear regression models that describe nitrogen stable isotope ratios in four trophic levels. TN = streamwater total nitrogen, %Qtz = percent of major rock type in subbasin as quartzite.

Species	Best-fit Model	Parameter	Coefficient	*p*
Periphyton	$0.04\ x_1 + 0.14\ x_2 + 1.37$	% Burned	0.036	0.0004
		Baseflow discharge	0.137	0.018
		TN	-0.003	0.115
Grazer	$0.26\ x_1 + 0.04\ x_2 + 1.97$	% Burned	0.255	0.0002
		Baseflow discharge	0.036	< 0.0001
		% quartzite	-0.013	0.109
Collector	$0.03\ x_1 + 3.90$	% Burned	0.034	0.007
Predator	$0.11\ x_1 + 0.04\ x_2 + 4.43$	% Burned	0.109	< 0.0001
		Baseflow discharge	0.044	0.016

Table 7. Summary and parameter estimates of the best-fit multiple linear regression model for nitrogen stable isotope ratios in stream periphyton and macroinvertebrates. TN = streamwater total nitrogen

Model	R^2	*F*	*df*	*p*	*k*	*AICc*	*ΔAIC* (Δ_i)	Model Likelihood	w_i
Periphyton									
Baseflow discharge + % Burned + TN + %Qtz + %Cover	0.5621	13.07	5,43	< 0.0001	7	1300.618	2.177	0.337	0.248
Baseflow discharge + % Burned + TN + %Qtz	0.5672	16.4	4,43	< 0.0001	6	1298.441	0	1.000	0.707
Baseflow discharge + TN + %Qtz	0.464	14.56	3,44	< 0.0001	5	1307.196	8.755	0.013	0.009
Baseflow discharge +TN	0.435	19.1	2,45	< 0.0001	4	1308.287	9.846	0.007	0.005
Baseflow discharge	0.258	17.38	1,46	0.0001	3	1320.02	21.579	0.000	0.000
Grazer									
Baseflow discharge + % Burned + TN + %Qtz + %Cover	0.604	15.32	5,42	< 0.0001	7	1282.873	1.982	0.371	0.203
Baseflow discharge + % Burned + TN + %Qtz	0.606	19.12	4,43	< 0.0001	6	1280.891	0	1.000	0.547
Baseflow discharge + % Burned + TN	0.57	21.8	3,44	< 0.0001	5	1283.595	2.704	0.259	0.141
Baseflow discharge + % Burned	0.546	29.26	2,45	< 0.0001	4	1284.83	3.939	0.140	0.076
Baseflow discharge	0.52	51.23	1,46	< 0.0001		1286.517	5.626	0.060	0.033
Collector									
Baseflow discharge + % Burned + TN + %Qtz + %Cover	0.5327	11.71	5,42	< 0.0001	7	1263.288	5.282	0.071	0.039
Baseflow discharge + % Burned + TN + %Cover	0.541	14.83	4,43	< 0.0001	6	1260.844	2.838	0.242	0.134
Baseflow discharge + TN + %Cover	0.5696	19.41	3,44	< 0.0001	5	1259.4	1.394	0.498	0.275
Baseflow discharge + TN	0.5396	28.55	2,45	< 0.0001	4	1258.006	0	1.000	0.552
TN	0.0668	4.364	1,46	< 0.0001	3	1290.594	32.588	0.000	0.000
Baseflow discharge	0.343	25.54	1,46	< 0.0001	3	1273.75	15.744	0.000	0.000
Predator									
Baseflow discharge + % Burned + TN + %Qtz + %Cover	0.63	15.61	5,38	< 0.0001	7	524.197	2.4	0.301	0.213
Baseflow discharge + % Burned + TN + %Cover	0.63	19.72	4,39	< 0.0001	6	521.797	0	1.000	0.707
Baseflow discharge + % Burned	0.52	24.53	2,41	< 0.0001	4	530.606	8.809	0.012	0.009
Baseflow discharge + % Burned + TN	0.5614	19.34	3,40	< 0.0001	5	528.3371	6.5401	0.038	0.027
Baseflow discharge + % Burned + %Cover	0.5711	20.09	3,40	< 0.0001	5	527.3471	5.5501	0.062	0.044

Table 8. Results of model selection using AICc for multiple linear regression models that describe carbon stable isotope ratios in four trophic levels. TN = streamwater total nitrogen, %Qtz = percent of major rock type in subbasin as quartzite.

Model (δ^{34}S)	R^2	*F*	*df*	*p*	*k*	*AICc*	*ΔAIC* (Δ_i)	Model Likelihood	w_i
Periphyton									
Baseflow discharge + % Burned + TN + %Qtz + %Cover	0.116	2.227	5,42	0.06928	7	-3.840	8.577	0.014	0.008
%Burn + %Cover + TN + %Qtz	0.136	2.848	4,43	0.03518	6	-6.583	5.834	0.054	0.017
%Burn + %Cover + TN	0.153	3.838	3,44	0.01589	5	-9.080	3.337	0.189	0.059
%Burn + %Cover	0.162	5.541	2,45	0.007056	4	-10.990	1.427	0.490	0.154
%Cover	0.164	10.2	1,46	0.002539	3	-12.417	0.000	1.000	0.314
%Burn	0.043	3.101	1,46	0.08489	3	-5.938	6.479	0.039	0.012
Grazer									
Baseflow discharge + % Burned + TN + %Qtz + %Cover	0.785	35.29	5,42	< 0.0001	7	350.147	3.664	0.160	0.077
Baseflow discharge + % Burned + %Qtz	0.786	58.67	3,44	< 0.0001	5	346.667	0.185	0.912	0.440
Baseflow discharge + %Qtz	0.781	84.71	2,45	< 0.0001	4	346.483	0.000	1.000	0.483
Baseflow discharge	0.094	5.887	1,46	0.01923	3	413.259	66.776	0.000	0.000
%Qtz	0.537	55.4	1,46	< 0.0001	3	381.101	34.618	0.000	0.000
Collector									
Baseflow discharge + % Burned + TN + %Qtz + %Cover	0.334	5.721	5,42	0.0004114	7	-283.373	5.818	0.055	0.019
Baseflow discharge + %Qtz + TN	0.353	9.538	3,44	< 0.0001	5	-287.860	1.331	0.514	0.178
Baseflow discharge + %Qtz	0.352	13.74	2,45	< 0.0001	4	-289.191	0.000	1.000	0.346
Baseflow discharge	0.301	21.23	1,46	< 0.0001	3	-286.909	2.282	0.319	0.111
%Qtz	-0.003	0.8533	1,46	0.3604	3	-269.578	19.613	0.000	0.000
Predator									
Baseflow discharge + % Burned + TN + %Qtz + %Cover	0.775	30.63	5,38	< 0.0001	7	321.312	0.000	1.000	0.314
Baseflow discharge + % Burned + %Qtz +TN	0.764	35.81	4,39	< 0.0001	6	321.718	0.406	0.816	0.256
Baseflow discharge + % Cover + %Qtz+ TN	0.759	34.84	4,39	< 0.0001	6	322.665	1.353	0.508	0.159
Baseflow discharge + %Qtz + TN	0.755	45.08	3,40	< 0.0001	5	321.865	0.554	0.758	0.238
Baseflow discharge + %Qtz	0.723	56.98	2,41	< 0.0001	4	325.809	4.497	0.106	0.033

Table 9. Results of model selection using AICc for multiple linear regression models that describe sulfur stable isotope ratios in four trophic levels. TN = streamwater total nitrogen, %Qtz = percent of major rock type in subbasin as quartzite.

CHAPTER 2

Creative nonfiction as an alternative approach to communicating scientific research: Integrating stream ecology research and wilderness narratives

Abstract

Science communication is becoming increasingly important given the current realities of a highly connected society in a changing climate. The demand for rapid communication of scientific study results has led to special releases of academic journals, streamlined communication and networking through online communities of scientists, and increased popularity of popular science media with the general public. The advent of these alternative modes of communication may mean that scientists with adaptable communication skills have a competitive advantage with respect to publicity, funding opportunities and publication potential. This chapter focuses on the utility of creative nonfiction as an alternative approach to communicating scientific research. With engaging, personal narratives from a field-based research study, this writing project educates the audience on stream ecology, cross-ecosystem subsidies and the importance of opportunities to conduct research at the intersection of wilderness and cutting-edge technology. This project adopts a process-based framework that focuses on developing disciplinary depth and breadth and interdisciplinary integration. The integration of

ecological research and nonfiction writing fits into a long tradition of science-based literary nonfiction. This project continues along the trajectory of that tradition and aims to shed light on a valuable process for promoting intellectual flexibility within academia and an effective means to disseminate results and bolster scientific literacy among broader audiences.

Introduction

> "I have come to believe, as the primary definition of these 'popular' essays, that the conceptual depth of technical and general writing should not differ, lest we disrespect the interest and intelligence of millions of potential readers who lack advanced technical training in science, but who remain just as fascinated as any professional, as just as well aware of the importance of science to our human and earthly existence." - Stephen Jay Gould

Societal, literary and scientific motives drive this interdisciplinary writing project, along with the belief that there is value in having the results of research projects go beyond the realm of scientific journal manuscripts. Creative nonfiction has great potential to augment the intrigue and impact of important ecological conditions and processes. A great deal of successful creative nonfiction science writing has come out in the last century by American writers such as Aldo Leopold, Rachel Carson, Gary Paul Nabhan, and many others. Here, I define successful authors as those who not only offer observations of the natural world and humanity, but dive into technical details of the phenomena they explore and integrate that information into narratives that are engaging for the reader. The most successful authors also effectively increase knowledge and scientific understanding of the topic among disparate populations, including non-scientific audiences.

The essays in this chapter aim to inform non-scientific audiences on stream ecology and cross-ecosystem subsidies, fostering holistic ecosystem thinking and attention to waterways as multi-directional corridors. They convey a message to readers, educating them on stable isotope ecology, its utility in measuring connectivity of disparate ecosystems, and how scientific inquiry promises to help in the future. This is worthwhile in light of the national focus on dam removals and river restoration in recent years. The use of stable isotopes to understand river connectivity and nutrient sources and sinks may become an increasingly important and common tool in restoration projects. Creative nonfiction allows room for the author to candidly alleviate confusion regarding scientific principles, policies, or processes. This is an important skill in the field of natural resource conservation as it can increase interest, comprehension and action among the public, policy makers, fellow researchers and funding providers.

There is evidence of an emerging need for the integration of science and public communication. Science communication courses and programs are growing in universities and colleges around the country. The National Science Foundation has funded projects that specifically focus on the interdisciplinary integration of creative nonfiction and science policy issues. The NPR program *Science Friday* is perhaps the most prominent of many alternative media outlets for public science stories that are increasing in popularity.

My narrative essays also offer cultural insight as they provide a way to share the experience of conducting research in the remote wilderness and illustrate Taylor Wilderness Research Station as a unique place in the West. The intersection of "old Idaho"–

where strong survival skills and remote community support enabled some of the earliest research on wilderness ecosystems–and "new Idaho"–where bush planes allow easy access and wireless satellite internet is enabling real-time regional networks of stream and climate data–offers great material to develop literary skills and engaging stories.

American nature writing has gone through many phases, from early explorers to the transcendentalists, to the more ethically complex environmental writing of today. The current renaissance in writing about the natural world is expanding it in multiple directions. Environmental literature, advocacy-driven journalism, ecocriticism, natural history, blogs, and even podcasts are developing quickly today. Much of the more traditional environmental literature shares nature as a place and as an experience, sometimes even exploring it as a complex component of humanity. This writing project focuses on sharing nature as an object of scientific study and seeks to explore the juxtaposition of the need to study “nature” analytically, while also inescapably developing a relationship with it and valuing that subjective experience.

The process of integration in this thesis follows the approach outlined by Repko (2008). Disciplinary adequacy was developed in each of three disciplines—stream ecology, science communication, and nonfiction writing—through relevant graduate level coursework, classroom instruction and personal studies. Strong disciplinary breadth was achieved in building common understanding and connections between the epistemologically distant fields of creative writing and ecology.

The project increased communication between two disciplines: 1) at the university level, by increasing English department faculty involvement in the interdisciplinary Waters of the West program; and 2) on a national level through conversation with successful American environmental authors Paul Bogard, Rick Bass, Janisse Ray, and Karsten Heuer. Finally, this project explored creative nonfiction as a viable outlet for scientific research, demonstrating to scientists that results can be shared in this realm without losing their meaning, helping all those involved maintain intellectual flexibility, and producing the following narratives that integrate knowledge and modes of thinking from epistemologically distant disciplines into a new entity.

Essay 1

4,000 x 2

4,000x2 was established in 1983, three years before I was even born, by scientist, hunter, mule-packing cowboy, Jim Akenson, partway through his 20-year stint living in the wilderness. Though this combination of professions seems unlikely to spawn hiking clubs, it’s not so far fetched when living 30 miles from the nearest trailhead makes hiking extraordinary distances part of everyday life.

I had secretly been eyeing the homemade placard in the lab all summer, partly because there is a basic error in the title that I was itching to fix, and partly because I wanted my name up there. “Hiking Club: 4,000’ ^{2}” it reads, which suggests you must hike

16,000,000 vertical feet to join the club. The kicker is the rule that it must be done during daylight hours only. Sunrise, hike Mount Everest 551 times, sunset. Yea right.

The wood-burned title should read “4,000 x 2” to accurately reflect the guiding principle of this hiking club, in which you must hike 4,000’ up the North side of the valley, return down to Big Creek, hike 4,000’ up the South side of the valley, and return to bottom before sunset. This still may not sound like an incredible feat given the ultra-marathon trail races, overnight high-altitude relays, and other superhuman athletic events that are popping up nationwide. After discovering every nook and cranny of all seven continents, the depths of the oceans, sending robots into outer space and dissecting the smallest known particle, we seem pushed to explore yet another frontier: the human body. But maybe we’re not all super athletes. Or maybe they haven’t spent time in the Frank Church-River of No Return Wilderness. Regardless, the hiking club at Taylor Wilderness Research Station remains a final frontier open to anyone who wants to explore the capabilities of their own body beyond the edge of civilization. Located 30 miles from the nearest trailhead in central Idaho right along Big Creek, a tributary to the Middle Fork of the Salmon River, the research station affectionately known as Taylor Ranch is not exactly a hot spot for destination travelers. Or athletes. Or really anyone, except avid fishermen, hunting outfitters, and the few scientists and academics whose work takes them there.

I met Jim Akenson in person last year and managed to earn a little nugget of respect from him during a long day of volunteer mule packing and hiking steep ridges to help some climate researchers haul heavy gear up the mountainsides (no mechanized transportation when working in the wilderness, and no exceptions). Jim is a man of few words, stoic as the next western rancher and not one ‘to blow sunshine up your ass’ even if you’re doing alright. He is the one that introduced me to that phrase, though. I put on my best serious cowboy voice and ask him about the hiking club.

“Only 18 people have joined the hiking club, seven of ‘em did the Peak to Peak challenge.”

“That’s less than one successful attempt per year!” I think to myself. Nobody keeps track of failed attempts, just as statistically insignificant scientific research never gets published—another gripe of mine for another time. I wait to see if he’ll go on, but apparently more prompting is needed.

“What’s the Peak to Peak?”

“You climb to the top of Dave Lewis Peak and Horse Mountain in daylight hours.” These are the two most prominent peaks in the area, one on each side of the valley, though a distance of about 7 miles as the crow flies separates their summits. With Dave Lewis Peak at 9,300’, Horse Mountain at 8,200’ and Big Creek at 3800’, that makes for a total of 9,900 vertical feet. Still not 4,000’ *squared* I think briefly to myself, then shake the slightly neurotic thought away as Jim continues. “Chris McDaniel was an intern with us one year here at Taylor Ranch, and he did three peaks in daylight hours. Earned himself the title of club president. I don’t think we’ve had any women complete the Peak to Peak, though…”

Once Jim said that there hadn't been a woman to complete the Peak to Peak yet, the wheels started spinning in my head. He knew it, too. Luckily I had been "training" by default all summer, hiking to various sites around the watershed for my stream ecology research, and on my off days running up the ridge trail—I love the views from up there as a nice alternative to always being down in the bottom of the valleys where my field work keeps me.

I didn't want to seem too eager, and I didn't want to talk the talk without hiking the hike, but I was fixated on it for the next few days. The day before Jim packed up his mules to head upriver, everyone at the research station was gathered around the campfire, chatting casually as you do when nobody has anywhere to be or any devices to check compulsively.

Jim turns to me, "You're a good hiker, Liza—you going to join the hiking club this year or what? The days are only getting shorter the longer you wait." I was a little surprised Jim had publicly commented on my hiking skills. I didn't even realize you could be a good or bad hiker. I just figured it was like walking and everyone knows how. But the other half of what he said was quite true. It was mid-August: I had already missed the longest day of the year and the summer hours were ticking away.

"Well, I don't have much to do tomorrow. I think I'll try it."

The managers of the research station and other researchers seemed a little surprised I hadn't given more warning about my upcoming attempt, but those that know me well know enough know not to be surprised by spontaneous adventures.

Unable to convince anyone else at the research station to join, I set off up Horse Mountain as the sun was creeping up the next morning. As I crested the first major ridge and the sun's rays were still horizontal, a huge whoosh right over my head startled me as I accidentally disturbed a golden eagle that had been resting on the other side of the rock hardly five feet away! Already I felt the hike was worth it—to hear the feathers open up and begin to beat against gravity, to feel the movement of air from its powerful wings on the brow of my forehead where beads of sweat had already started to form. I was motionless as the bird soared away, farther and farther, until it became a speck that disappeared into the background of charred trees on a distant hillside burned by the wildfire that swept through this valley not long ago.

A bit later I heard rocks crumbling above me and bouncing down the rock outcrop I was climbing along. A group of sheep—five females and two young ones with short horns just starting to push their way into the world—were also working their way up this rock outcrop. I followed them for about half an hour, innocently pushing them upwards as I climbed, my nostrils full of their musky scent whenever I got close. I had never experienced a smell like that and wondered if all my time in the wild fresh air had helped me start to pay more attention to the subtleties in all my senses.

The burning began in my calves. With no trail leading up this mountain and the awareness of another mountain awaiting me after this one, I opted for the "straight up" route. Near one of the false summits I quite literally scrambled face first into a raspberry patch in the midst of the talus fields. The bushes themselves were quite small, but the thorns were not. Soil was more or less nonexistent, but the berries had the most brilliant flavor I’ve ever experienced. The contrasts are glaring in this country, and they spread from the smallest raspberry bush to the climate that determines the character of the environment. The morning fog, and its associated chill, had burned off, and was quickly being replaced with an inescapable heat. I also realized that my pace had become subject to the rule of contrasts as I had come to a screeching halt while I plucked the tiny, juicy berries and popped them into my mouth. I tore myself away with the recollection that I had places to walk that day and scuttled on.

I remember sliding down the cheat grass-covered scree fields back near Taylor Ranch before noon, feeling like a wild animal with every muscle acutely ready. A 15-minute stop with my feet up in the shade, scarfing down a sandwich before the assistant manager accompanied me about a mile up Pioneer Creek to show me the way he thought best to approach peak number two.

Following him for that mile, it dawned on me that I had never been up either Horse Mountain or Dave Lewis Peak before. That was part of the challenge and adventure for me, and when he stopped and sent me up the ridge with a good luck handshake, I felt the freedom of being alone again. While I do wish for company on these endeavors sometimes, I am happy to have the capabilities and confidence as a young woman to embrace and enjoy the solo adventures.

Dave Lewis Peak lacks the steep talus fields and broken bedrock outcroppings of Horse Mountain, and evidence of a trail appears and disappears a number of times. A novice naturalist could detect that the ridge I was following had seen pack strings of horses and mules, hauling hunters loaded down with rifles, hot dogs and whiskey. The area is occasionally visited by outfitters that are permitted to hunt in this part of the wilderness—the odd horseshoe, decaying manure, and abandoned fire rings are welcome clues that I am on the right path.

I found it impossible not to manically seek out portions of trail—even fifty yards on an old game trail was easier walking than clambering over burned stumps, rocky terrain and through windfall. A large wildfire swept through this region in 2000, forcing all residents, recreationists and researchers to flee from Taylor Ranch and changing the landscape dramatically. It was hard for me to imagine the same hike through a thick evergreen forest. The day had gotten hot. Hot and smoky and sticky. The wind shifted around noon and blew smoke from a distant wildfire into the Big Creek drainage. It grew thicker and cut off the views into the deep drainages surrounding me, leaving the ridge I was walking along to fall off on both sides into an ominous oblivion.

I had a GPS with me and was thrilled to meet the 4,000ft elevation gain on the second peak. Finally, I felt like I wouldn't be a failure if I decided to turn around...but the Peak to Peak (or Jim Akenson’s personal challenge, as it had become in my head) drew me onwards and upwards along the long ridge. I reached the first false summit and genuinely thought about calling it the real one—nobody was with me, and who would know the difference? Guilty conscience and remembering the GPS I had with me snapped me out of wishful thinking and back into power-hiking mode. I snapped a picture of myself and marked a waypoint at the true summit and headed down immediately. I could tell I was moving slower now and sometimes would just instinctually sit down for a second to stretch my legs and body. There was another reason it was nice to be on hour 10 of a hike through beautiful country and no chance of crossing paths with anyone—my shorts had starting chafing badly on the descent and so, being a pragmatic individual, I had taken them off!

I made it back to Taylor Ranch with daylight to spare, pants back on for modesty's sake, and sat on the porch of the old log cabin. It felt wonderful to be so still after 13 hours of nearly non-stop hiking, and I imagined this is what Dave Lewis, the outfitter who had built this cabin by hand in 1911, might have felt like after just one day of work. Odd, isn't it, how the daily challenges of yesteryear are comparable in effort to the once-in-a-lifetime challenges of today? Then again, he was a grown man raised in that lifestyle, and I am a twenty-something, Patagonia-wearing, budding female scientist exploring the peripheral opportunities of this profession. Who am I to evaluate anything but my own experiences in the world?

Tired, dirty, and salty, I sat there looking up at Horse Mountain across the valley with a new knowledge of those rocky outcroppings and all the surprises they hold for those willing to say, "Yes!" Humility kept me from inscribing my own name into the wooden placard, but as I watched the evening progress into night I was very proud to be the first Peak-to-Peak lady. And particularly charmed with the idea that I was probably also the first person of any gender to do half the Peak to Peak challenge with no pants on!

Essay 2

Contrary to Convention: Up the river and tracing the invisible

You know the feeling that frantically runs through your body the split second after your alarm starts going off? It's worst when you've had that same cell phone jingle as your alarm for years. Any sound that begins at that frequency makes you jump and strike out towards the snooze button. It was 5:30 a.m. and still dark out when I heard that noise and lashed out, only to find myself constricted in a tangle of sleeping bag zipped up to my nose. I quickly reconstructed my life and realized I was not, in fact, bobbing for apples that inevitably turned to clown noses as my dream mind insisted. Rather, I was huddled in my down sleeping bag, alone on the ground next to my car on the banks of the Salmon River under a starry night sky. I'd made a 90-degree turn in the night and only my shoulders remained on the sleeping pad, my head and lower body on the dirt and gravel of the pull-out I'd desperately chosen a few hours earlier when I found myself nodding off behind the wheel. Fumbling with the pull cord I'd over-tightened I hastily ripped the sleeping off me without bothering to unzip it. My phone flew across the ground but continued its insistently cheery chiming of bells. Finally putting a stop to it, I shook off the sleepiness, shoved the sleeping bag and pad into the back of the car and started the engine of my trusty Silveru. Silveru? It was a silver Subaru, named so by my mother, of course.

A moment later I was rocking down Highway 95, licking my fingers as I ate one of the first juicy nectarines of the season, doing some mental math to make sure I would get to the Cascade airport before my scheduled flight into the backcountry. At least it wasn't a real airport, with parking and check-in, security lines, schedules and overly sanitized bathrooms. I knew Walt, the pilot, would be patiently waiting next to the Cessna 206, checking his watch and slowly loading the plane with boxes of frozen food that he would deliver to all the small communities scattered throughout Central Idaho's vast roadless area after he dropped me off at Taylor Ranch. 160 miles to go, at 65 mph, with the hour time-change when I crossed the Salmon River Bridge near Riggins…. Maybe when I get back into phone service I will call Walt and tell him I'll be about 20 minutes late.

Then it happened. Anyone who has lived in rural North America knows what I am talking about, either from first-hand experience or from stories shared around a campfire. Deer. Three big bucks. On the road. Let's fast forward to the part where I crawl out the driver's side window to stand on side of my car, hair tussled but overall uninjured, waving my hands frantically in the headlights of an oncoming semi-truck. Let's fast forward again to the part where I am standing in the chilly air explaining my master's research project to the truck driver, patiently waiting for another car to pass to send for help. Cell phones, 3G networks, even two-way CB radios … all those technologies were worthless down there in the canyon where the river flowed steadily past, exerting its subtle force on the landscape. We were forced back to good old-fashioned conversation to help pass the time.

"Sooooo," he has a long drawn out way of speaking. I can tell he is from northern Idaho. "What is it you do to figure out if the nutrients are from the salmon or not?"

I had just practiced my “elevator speech” on him, trying to summarize in two quick sentences the complex chemistry of stable isotopes and the ecological connections that I was preparing to research for the next two years of my life. And now he was actually asking me questions about it? There we were looking at the remains of my car in the grey, pre-dawn light, surrounded by shattered glass, and miscellaneous bits of scientific equipment that had freed themselves from their nicely packed positions in the car and scattered out onto the road. I clearly just had a near-death experience and he is inquiring into my methodologies and research logistics? While part of me was taken aback by the mundane nature of our conversation, wishing to give the moment the weight it seemed to deserve, I was in no place to steer the conversation back to car crashes. While the “what ifs” and “what nows” continued to run rapidly through one half of my brain, I start to share the story of salmon populations in central Idaho to my new guardian angel truck driver.

The life cycle of salmon is a fairly well known story these days but it never ceases to amaze me. The vast distances these fish travel from the inland headwaters out to the salty Pacific where they reside for a few years. The predators, degraded habitat, water pollution, and barriers to migration they encounter a second time as they swim hundreds of miles upstream to return to the exact location they were born. And all in the name of what? Reproduction, I suppose. Like every species on the planet, they have evolved unique strategies to facilitate the success of their offspring. It took scientists years to unravel the migration of these creatures. Researchers are still trying to explain it quantitatively with bioenergetic models that categorize fish activity into a complex cost/benefit analysis. The abundance of high-quality food resources in the ocean is a stark contrast to the cold freshwater streams where these fish dwell as juveniles, so the salmon have in essence decided that the rewards of migrating to and from these distant resources outweigh the risks.

We don't need to anthropomorphize salmon to death, we've done enough damage through overharvesting, hatchery production, habitat degradation, and dam construction and operations. Nevertheless we can recognize an incredible life history; their resiliency is to be admired, and it is easy to become passionate about them and mystified by it all, even as you wait for a policeman and tow truck to pull you out of a ditch.

"When the adults come back from the ocean to these headwater streams where they were born, they are much much bigger than when they left!" I find myself caught up in the story for the umpteenth time, using hand gestures to show him how much they grow and demonstrating a moment from the previous year when I found a carcass that was over a meter long and too heavy for me to pick up with just one hand. "But all they do is spawn and then die. All that mass they accumulated in the ocean now remains in a very different ecosystem."

I wanted so badly for him to understand this idea of cross-ecosystem subsidies, to really get how interconnected everything in this world is, to believe in the cycles and variability and wild unpredictability that is the most natural part of our world. But I have spent years in school studying the theories, convinced by case studies, influential mentors, and my own experiences wandering the wilds of the world. And during all those years Mike has been delivering timber to lumber mills.

“Soooo, whatchur saying is that those dead salmon might be fertilizing the stream the same way a farmer fertilizes his fields?” His slow speech is an abrupt contrast to my rapid rambling but he has an impressive ability to jump to subsequent issues. He should be a scientist I think to myself. And I take his curiosity as permission to dive into the real detective work I plan to do.

Ultimately I want to figure out if the nutrients released from the decomposing carcasses make their way into the local food web. In ecology this would likely be referred to as a pulsed resource subsidy, since the salmon all spawn and die within the span of about a month in late summer each year. In management and policy circles this would probably be discussed in terms of nutrient enrichment, as that is the end result they are looking for. I realize now that in everyday life, *fertilizer* gets the point across. Sometimes it is depressing to spend so much time working on things that don’t matter to the majority of people out there, and it is only of marginal comfort to know that this is an incredibly common sentiment in the field of scientific research. That’s why folks like Mike are so refreshing. They make you pull your head out of the jargon tunnel, academic hoopla, and statistical computer programs to rediscover the magic that brought you into science in the first place.

And it really is a little bit like magic. The nitrogen molecules inside the adult salmon, which came from a marine environment, have a different chemical signature than the nitrogen that is found in the local headwater ecosystems. Stable isotopes provide this chemical signature that helps reveal the origin of nitrogen, or carbon, in any living creature.

"Isotopes," I break down the etymology of the word for him, "*iso* means equal, as in isosceles triangles that have two equal-length sides. And *topo* means place or location, as in topography. Together it means same place, referring to the fact that they come from the same place on the periodic table." Stable isotopes are used as natural tracers of carbon, nitrogen, and other elements in medical, forensic, and natural science fields. With utility for a wide variety of purposes, stable isotopes remain just as they are forever, unlike radioactive isotopes such as uranium that decay over time, changing into different forms.

Any evidence of marine derived nitrogen, identifiable by the unique ratio of stable isotopes, in the algae or aquatic insects at my research sites where salmon are present would suggest that the salmon do have a fertilization effect on the system. As salmon populations continue to decline in the Pacific Northwest, better understanding of this fertilization effect is sought after by scientists, managers, tribal nations, anglers, and other engaged citizens.

For studying something that is supposedly stable, my research experience has often been on the verge of mayhem. I am a scientist. Must mean I wear a white coat and glasses, work with very controlled amounts of very complex compounds, and focus on mechanistic understandings of our world. Wrong, wrong, wrong. Let me take you on brief journey: my first major sampling campaign as a self-directed scientist. I had the research question and the methods, I had the equipment, the field technicians, the enthusiasm, and most importantly, I had received a slight nod from my major advisor, which I took as a blessing to go forth and find answers! Finally ready to spread my wings and fly into this wilderness graduate research adventure in earnest, I got flown from the research station to the upper part of the watershed, where there is a trailhead at the end of a 90-mile dirt road. My field techs were there waiting for me.

I felt a little bit like a modern day Ernest Shackleton earlier that spring when I sent out the following announcement to all my graduate student friends, acquaintances, and their friends, too:

> “Wilderness Wadgers wanted:
> A ‘wadger’ is a badass creature that is part wolverine, part badger, and part really awesome volunteer field tech. They can only be found in the Frank Church-River of no Return Wilderness, usually along the banks of Big Creek , and only during three discrete weeks each summer. As a professional wadger trainer, I have begin the hunt.
> Please note, if you choose to join the hunt you may or may not find one, may or may not become one, and are definitely not allowed to shoot one. Pay is non-existent, but as compensation you get to kayak or backpack down Big Creek and I will pay for your flight out from the most remote research station in the lower 48. Dates are not set in stone, ever, when working in the wilderness, so some degree of flexibility is key, as is the ability to work long days in beautiful country without complaint. ”

I got willing responses from a few brave souls. Only Ben was a true volunteer, motivated by the fishing opportunities. Rick was my lab manager, and Emily was another graduate student I was collaborating with, but so far all three had followed through. Apparently as an expedition leader I have a sink-or-swim approach. On the first day we had to hike two kayaks, four paddles, scientific equipment, personal backpacks, and paddling gear five miles down the trail to a place where we could put in onto Big Creek. Collapsing in the shade after the second trip of heavy awkward loads we unroll the two inflatable kayaks and…gasp…they aren't the same size. In fact the red one is only a one-person kayak.

Given our location, our resources, our needs, there was but one obvious choice. Vote someone off the trip. Or…make it work. Big Red, ironically named, was the one-person inflatable kayak that carried Emily and Rick, while the two-person Blue Barge carried Ben, myself, and about 250 lbs of gear. We deflated the seatback compartments to give ourselves room to sit, and whoever was in back could barely see anything over the pile of gear. There was a great deal of bumping along the rocky river bottom, pulling the overloaded boats over log jams that spanned the width of the river, and a few unexpected capsizes. I tried hard to keep morale up and control the chaos.

Some weathered the mayhem better than others, but once we were floating more smoothly, we started laughing. A bit of perspective and the ability to take yourself not too seriously is often all it takes to make life extremely enjoyable and hilarious. The water was clear and cool, slipping effortlessly over the rounded river rocks. We learned to recognize the darker portions of the channel indicating the thalweg—the deepest part of the river channel. It never runs dry here so the algal composition on the rocks is slightly different and thus a helpful clue as to where we might find the fastest flows.

I watched the creek grow as trickles of various tributaries joined our downstream exodus. Always flowing downhill, downstream. How predictable. How consistent the movement, but how changeable the material. As the water flows it picks up qualities from its environment. Sediment from the hillslopes, banks, and streambed join the moving water during hard rain and high flows. The metabolic processes of life—growth, excretions, death, and decay of plants and animals alike contribute important nutrients to the riverscape. While carbon and nitrogen molecules dissolved in the water are only detected in elaborate water chemistry labs, and particles of organic matter suspended in the turbulent flow are visible only to the insects and fish that feed on them, it is an obvious conveyor belt of downstream movement. Except the salmon! While everything else in the stream network is submissive to the force of gravity, the salmon defy it. Using the fat and energy reserves stored in their bodies, these Chinook salmon fight and wiggle and swim and splash their way up the Columbia River, up the Snake River, the Salmon River, and into Big Creek. I want to encourage each big fish I see holding and resting in a deep pool or eddy, contradicting all signs that down is the way to go.

It is wonderful to be inspired again to pursue a better understanding of the role these fish play in this central Idaho watershed. What does it mean for the local plants, insects, fish, birds and bears that these creatures are challenging the assumption that rivers are corridors of unidirectional movement? I feel empowered with the scientific knowledge of today and tools like stable isotopes to try to detect marine derived nitrogen in the local ecosystem. I hope I can write my guardian angel truck driver someday to thank him. And to tell him if the salmon are fertilizing the headwaters streams of his home state.

Graduate school. It doesn't have to be cutthroat competition in classes, late nights with gallons of coffee in the library, and stress to make your hair turn gray. It may, perhaps, be cutthroat trout fishing, late nights with gallons of pure creek water flowing past you, and a supportive network of wadgers to minimize grad school stress and enjoy life itself.

The rhythmic movement of the paddles dipping into the clear water and the sound of water droplets falling off the blade back into the river as it slices forward through the air for another stroke. It all makes me feel so alive, so alert, and so wonderfully removed from the rat race of iPhone reminders, tangled charger cords, and social obligations.

I think about the river otters that we watched gracefully slither through the moving water yesterday evening while scrubbing the algae off of river rocks to wrap up the day's sample collection. How capable and graceful they were in comparison to us hauling half-inflated kayaks through log jams and up onto the bank! How they can understand water quality without taking samples and shipping them off to a distant laboratory. How they can sense changing weather patterns without barometric pressure sensors. It makes me almost embarrassed to be a human. Even when trying to do what's best, reliant on our own technologies, we still make an awful lot of mistakes. We still use the wrong chemicals on our fields, we still build dams in the wrong places, we still try to predict the dynamic balance of natural systems, and we still forget batteries for the flow meter.

We may be a blundering species, but I am thankful to be in a place where I can be so vividly reminded of that. A place where I can still try travelling through rugged country, attempt to understand the dynamics of a stream ecosystem characterized by declining salmon populations, and do the best I can.

Essay 3

In A Backwoods Way

An argument in favor of wilderness education and research

I pull up to the airport in Cascade, Idaho. I am not sure where the line is drawn between an airport and an airstrip, but I believe this one sits right on that line. The fact that is has a fully paved landing strip, with painted lines on it, and there is a little office next to the hangar with a sign reading “Arnold Aviation,” makes me want to call it an airport. Other features make me want to call it a landing strip. First of all: no tickets required—just call up Carol’s landline and see when they have flights going into the Big Creek drainage. If they have room for you, she’ll write your name in pencil onto their big old calendar that sprawls over the main desk and determines the schedule of their lives. Also, no security or bag check—you can bring *anything* you want. And people do. From dogs, cats, parrots, red-tailed hawks, and dead cougars and sheep to rifles and bows, machetes, large amounts of denatured ethyl alcohol and diesel wood chippers, these guys will fly it all, few to no questions asked. The first few times I flew with them, it felt like traveling back in time. While I have been on a few bush plane flights before up in Alaska, in actuality I am a welltrained, 21st-century commercial airline client, hardly blinking at long security lines and robotically moving through the shoe, belt, laptop, no-liquids-more-than-3-oz shuffle.

Walt, the quiet pilot who has packed my gear for the summer into the little plane, finally asks me, "What is that that thing for anyway thatcha always got with you?" He was pointing to the telescoping steel rod, about a meter long that is one component to the flow meter that I use at all my research sites. Walt could be a prominent bush pilot anywhere in the world, skilled enough in his Cessna 206 to navigate steep valleys and flashy lightning storms and make one-wheeled landings on a slippery grass landing strip next to a flooding river. But his home is Cascade, Idaho, and he's not the type to leave home. After a fifty-minute flight over snow-capped peaks, winding river networks, and whole mountainsides charred by recent wildfires, we make the famous landing at Taylor Ranch where he drops me off with a smirk and a nod.

I fall asleep to the sound of sprinklers watering the pasture and wake up to small airplanes buzzing hundreds of feet overhead as they come in for a landing while the mountain air is still and cool. Is this really the wilderness? No, technically, I guess not. We seem to be all about technicalities in the West, especially when it comes to land and water. This little patch of land in the middle of the Frank Church-River of No Return Wilderness is one of those technicalities. Wild and luxurious, untrammeled and manicured, stuck in the 1800s and spawning cutting-edge technology: the Taylor Wilderness Research Station is full of juxtapositions. This is the second summer I have spent at the most remote research station in the contiguous United States, 30 miles from the nearest dirt road, hundreds from the nearest paved road or year-round residence. The more time I spend here, the more apparent the contrasts become.

In the mornings I venture to my research sites on nearby tributary streams. The same way children have their favorite haunts in the neighborhood and imaginary forts under the branches of a weeping willow tree, the research scientist has her study sites. I know to start the day at Rush Creek where I can soak up the warmth of the morning sun on that little patch of old river between the alder trees. I dread going to Cliff Creek, where the steep gradient creates cascades of white water over boulders and cobbles that are pleasing to the eye and ear, but treacherous for the foot that must walk across their slippery surfaces to collect water samples. It is a bit silly, really, the risks we take for one more tidbit of information about the system. I choose not to tell mom about the time I just *had* to finish calculating discharge while the lightning grew steadily closer, wading slowly across the river holding a stainless steel rod above my head. But it is a lesson in duty, devotion, and delayed gratification that the field scientist learns quickly. I dread the moment in the middle of the winter when I might kick myself for not spending five more minutes there to get an accurate reading and instead have a significant gap in my data.

In the afternoon, summer thunderstorms sweep through the valleys in a powerful, predictable fashion. Spending so much time in the same place, I become more aware of subtle changes. I make no claims to be able to read the weather in this volatile mountain climate, but it becomes less of a mystery to me that wild animals know to seek shelter well before any of us have thought to confirm the presence of a rain jacket in our backpack. The sky turns a shade darker, somewhere beyond the high mountain horizon that surrounds me, particles of water are gathering together, planning an attack, and scattering the sunlight that seeks to beat directly down on this rugged landscape. The breeze shifts ever so slightly.

When the building clouds reach the tipping point and topple over, crumbling down to the earth in big slow droplets, I retreat to the confines of the cabin. I shed my expensive, name-brand backpack and rain jacket at the door of my summer abode and walk into a log cabin built in 1911 by one man and one ax. The original cast iron stove is the only source of heat, but in order to find the matches and kindling I flip a light switch that turns on five light bulbs, driven by electricity gathered by the solar panels down in the pasture and stored in a large battery system. Every act in the day draws together two disparate time periods, two disparate ways of life, and I find myself constantly challenged to identify which mode of living I value more, or if the two can somehow be resolved.

A similar contrast runs through my professional endeavors conducting ecological research in the wilderness. Science—the discipline of analytical theory testing and prominently objective work. Wilderness—where unpredictability is the name of the game. During my final two month stint in the woods, I was evacuated twice for different wildfires, was on the lookout for an “armed and dangerous” Californian kidnapper roaming the wilderness with his victim on the run from the law, was charged by a rattlesnake nearly as long as I am tall—which isn’t tall for a person, but is long for a snake—lost two pieces of vital research equipment to the swift waters of big creek, and pulled one research technician out from his flipped kayak. To name a few minor mishaps.

Now try to run a statistical analysis with an unbalanced design. Now try to explain to a roomful of professors with a critical eye at your thesis defense why you have a missing value for one of your sites. I don't realize the weight of these other considerations until I am back in Moscow, spending days at a time in front of a computer crunching numbers or in the laboratory grinding aquatic insects into a fine homogenous powder for chemical analysis that will help me trace the fate of salmon derived nutrients through the food web. I spent so many years in the classroom learning about predictable natural processes, patterns and protocols. I planned and prepared to face every obstacle that the field season might throw at me. And yet now I feel that the unpredictability of nature and humanity is the only constant.

In many ways, the realities of doing research in remote areas make it a less-than-ideal place to conduct your first research project as a new scientist. But also for me, it reinforced the reasons I was drawn to ecology in the first place. The connections between the biotic and abiotic worlds are strikingly obvious when you live amidst them. In this realm, I find a place where all the contradictions and questions fall away: I use the personal connection I have to this place to motivate my analytical approach to sample collection, lab work and data analysis. This wilderness research offered a unique opportunity to travel back in time and explore the natural world the way that Darwin, Lewis, Clark and other early naturalists did, but fall back on trusted ecological theories to offer insight and explanations to the patterns I find. Perhaps we could all be better scientists, and writers, if we were lucky enough to go on this capricious ride with nature: to find that delicate balance between objective research and intimate connections with your studies.

The sun is setting, filling the smoke-filled sky with an orange blaze that mimics the flames of a wildfire a few drainages away. Time to hike back down this rocky ridge and wade across the river to my cabin so I can send an email into town and request that some more batteries, and maybe an extra chocolate bar, be delivered on the plane that's coming in tomorrow.

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