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Published online: 15 Feb 2017.

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Terrestrial–aquatic linkages in spring-fed and snowmelt-dominated streams

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ABSTRACT

The importance of trophic linkages between aquatic and terrestrial ecosystems is predicted to vary as a function of subsidy quantity and quality relative to *in situ* resources. To test this prediction, I used multi-year diet data from Bonneville cutthroat trout *Oncorhynchus clarki Utah* in spring-fed and snowmelt-driven streams in the high desert of western North America. I documented that trout in spring-fed streams consumed more (number and weight) aquatic than terrestrial invertebrates, while trout in snowmelt-driven streams consumed a similar number of both prey types but consumed more terrestrial than aquatic invertebrates by weight. Trout in spring-fed streams consumed more aquatic invertebrates than trout in snowmelt streams and trout consumed more terrestrial invertebrates in snowmelt than in spring-fed streams. Up to 93% of trout production in spring-fed streams and 60% in snowmelt streams was fueled by aquatic invertebrates, while the remainder of trout production in each stream type was from terrestrial production. I found that the biomass and occurrence of consumed terrestrial invertebrates were not related to our measures of *in situ* resource quality or quantity in either stream type. These empirical data highlight the importance of autotrophic-derived production to trout in xeric regions.

Introduction

Trophic linkages between aquatic and terrestrial ecosystems are ubiquitous, but the relative importance of these linkages can vary across space (Marczak et al. 2007; Marcarelli et al. 2011). In some recipient systems, terrestrial subsidies dominate the diets of aquatic consumers even when terrestrial subsidies are rare (e.g. Kawaguchi et al. 2003), while in other recipient systems these subsidies are largely ignored despite being readily available (e.g. Griffith Jr. 1974). Identifying aquatic habitat conditions that mediate the use of terrestrial subsidies is critical for effective conservation because terrestrial subsidies can influence the distribution, abundance, and growth of aquatic consumers (Nakano et al. 1999; Baxter et al. 2005).

The relative importance of trophic linkages in recipient habitats is predicted to be a function of the quantity and quality of the subsidy relative to *in situ* resources (Marczak et al. 2007; Marcarelli et al. 2011). Recipient consumers select trophic subsidies when they are more abundant, energetically greater, or easier to capture and assimilate than ambient resources (Wipfli 1997; Nakano, Kawaguchi, et al. 1999; Wilson et al. 2014). For example, the proportion of terrestrial invertebrates in fish diets peaked in the summer, when terrestrial invertebrate inputs to the stream were high in forested and grassland stream reaches (Kawaguchi & Nakano 2001). Experimental manipulations of terrestrial

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inputs underscore the importance of subsidy quantity, as fish shifted consumption to aquatic invertebrates when terrestrial arthropod inputs were reduced (Nakano et al. 1999; Baxter et al. 2004). Fish consumption of abundant terrestrial invertebrates is further reinforced by their high quality, including their larger size, greater mass, and higher nitrogen-to-carbon ratio relative to aquatic invertebrates (Wipfli 1997; Hilderbrand & Kershner 2004; Courtwright & May 2013).

Support for a positive relationship between trophic linkage importance to fish and the ratios of subsidy quality and quantity to *in situ* resources is well documented, but largely limited to forested, north temperate streams (reviewed in Marczak et al. 2007; Marcarelli et al. 2011). Indeed, the hallmark studies on trophic linkages between trout and terrestrial invertebrates occurred in a cold-spring-fed stream that flows through a temperate forest in northern Japan (e.g. Nakano et al. 1999; Baxter et al. 2004). In many of these forested streams, dense canopy cover contributes large allochthonous inputs while shading out autotrophic production; this imbalance can result in net-heterotrophic systems with low *in situ* resources (Minshall 1978). Much less is known about the relationship between trophic linkage importance and the ratios of subsidy quality and quantity to ambient resources in systems where autotrophic production may dominate, such as xeric regions or larger rivers (Minshall 1978; Minshall et al. 1985). A frequent criticism of stream ecology principles, like the River Continuum Concept (Vannote et al. 1980), is that models developed in forested, north temperate streams have limited applicability to different stream ecosystems (Winterbourn et al. 1981; Junk et al. 1989). However, testing generalizations across disparate habitats is critical to advancing predictive understanding, as exceptions to the rule can provide insight into important processes.

Here, I use multiyear, empirical data to test if the contributions of terrestrial invertebrates to stream fish diets vary as a function of *in situ* resources in high-altitude desert spring-fed (hereafter spring) and snowmelt-dominated (hereafter snowmelt) streams. In general, high-altitude desert streams have greater autotrophic production potential than forested streams because they have relatively sparse canopy cover and receive large solar inputs (Minshall 1978; Minshall et al. 1985; Resh et al. 1988). Spring streams receive the majority of their volume from groundwater, so exhibit dampened seasonal and temporal variation in temperature, flow and chemistry (e.g. Godwin & Carrick 2008). These conditions can increase instream primary productivity and provide year-round availability of abundant aquatic invertebrates (William & Hynes 1974; Laudon et al. 2005; Boulton et al. 2010). Because of this high-quality autochthonous production, aquatic invertebrates can dominate fish diets in the summer (Laudon et al. 2005). Seasonal secondary production in snowmelt streams is less consistent because of greater variation in temperatures, flow and nutrients (Robinson & Minshall 1998). If the difference between the quantity and quality of terrestrial invertebrates relative to aquatic invertebrates is larger in high-altitude desert snowmelt streams than in spring streams, then the contribution of terrestrial invertebrates to fish diets should be greater in snowmelt streams.

To test this prediction, I compared the contribution of terrestrial and aquatic invertebrates to Bonneville cutthroat trout *Oncorhynchus clarki Utah* diets relative to *in situ* resources in spring and snowmelt streams in Great Basin streams of southeastern Idaho. Bonneville cutthroat trout are native to Utah and parts of Idaho, Wyoming, and Nevada, and listed as a sensitive species in their native range. In forested, snowmelt streams in their native range, terrestrial invertebrates dominated Bonneville cutthroat trout diets in summer even when aquatic prey were prominent (Hilderbrand & Kershner 2004). However, there is little information on cutthroat diets in spring streams even though the buffered temperatures and flows of spring streams are likely to provide critical refuge from anticipated climate change impacts (Williams et al. 2009). An improved understanding of the relative importance of trophic linkages in different stream types may provide insight for native trout conservation strategies.

Methods

I used existing data on trout diets, terrestrial invertebrate inputs, and aquatic invertebrate availability from three spring and two snowmelt streams in the Bear River basin in the Great

Basin desert of southeastern Idaho (Table 1). These data were originally collected for other research objectives (e.g. Sepulveda et al. 2015), so a limitation of using these data is an unbalanced study design. Only two streams were sampled annually for four years (2011–2014), while the remaining four streams were sampled for 1–3 years within this time period (Table 1). These data provide a unique opportunity to describe how trout consumption of aquatic and terrestrial insects varies in disparate stream types.

Spring streams include Spring Creek, Liberty Creek, and Whiskey Creek, and snowmelt streams include Stauffer Creek and Pearl Creek (Figure 1). Within Stauffer Creek, samples were collected from two reaches, Upper Stauffer and Lower Stauffer, which were separated by ∼3.2 km. For this study, I treat these two reaches as independent sites. At each site, trout and invertebrates were sampled from 200 to 600 m reaches (Table 1). All samples were collected the last week of July, from 2011 to 2014. Access difficulties did not allow for annual sampling at all sites (Table 1).

Spring Creek, Liberty Creek, Upper Stauffer Creek, and Lower Stauffer Creek are adjacent streams in the same drainage (Figure 1). Whiskey Creek and Pearl Creek are located 20 km west and 12 km northwest, respectively, of this drainage (Figure 1). All of these streams are dominated by private, agricultural, and rangelands in the valley bottoms and forested, federal lands in the headwaters. Shrubs and herbaceous plants are the dominant land cover for Spring Creek (64%), Liberty Creek (64%), and Whiskey Creek (59%) drainages. Forests are the dominant land cover for Stauffer Creek (69%) and Pearl Creek (79%) drainages. The spring stream study sites are first-order, low-gradient streams but have different physical habitats (Table 1). Liberty Creek is shallow and narrow, Whiskey Creek is wide and deep, and Spring Creek is intermediate of the two. The snowmelt stream study sites are second-order, medium-gradient streams and have similar physical habitat (Table 1).

Trout consumption

I used diet data to describe the relative importance of aquatic and terrestrial prey to trout. Trout were captured with a backpack electrofisher and then measured (total length, mm) and weighed (g). For a random subset of trout (Table 2), stomach contents were sampled using gastric lavage and preserved in 95% ethanol (Barrow et al. 2008). Rhithron Associates (Missoula, MT) identified diet samples to the lowest practical level (genus or species), classified taxa as aquatic or terrestrial in origin, and counted and weighed (blotted wet weight) each identified prey item. I used these data to calculate (1) aquatic and terrestrial diet weight standardized by trout total length (mg mm^{-1}) for each individual, (2) the number of aquatic and terrestrial individuals per diet standardized by trout total length, and (3) the trophic basis of production (TBP), which estimates the contributions of different prey to trout production.

Table 1. Physical characteristics of the sampled stream reaches. Wetted width, depths, and flow are averaged across all four years of the study. Water temperature is the annual average during the period of study for all reaches except Whiskey Creek; the numbers in brackets indicate minimum and maximum values. Water temperatures from Whiskey Creek are the minimum and maximum values measured on 8 May 2011.

Stream type	Stream	Reach length (m)	Elevation (m)	Wetted width (m)	Depth (cm)	Flow (m s^{-1})	Gradient (m km^{-1})	Water temperature (°C)
Spring-fed	Spring	600	1826	3.6	11.1	0.03	5	7.2 [0–18.1]
	Liberty	200	1826	1.4	10.9	0.02	6	7.0 [0–21.0]
	Whiskey	600	1568	7.0	31.6	0.12	4	13–16
Snowmelt	Upper Stauffer	600	1848	2.4	8.9	0.09	18.3	7.2 [0–22.1]
	Lower Stauffer	200–600*	1821	1.9	10.6	0.07	10	6.8 [0–25.3]
	Pearl	200	1904	2.8	8.6	0.02	25	5.6 [0–18.0]

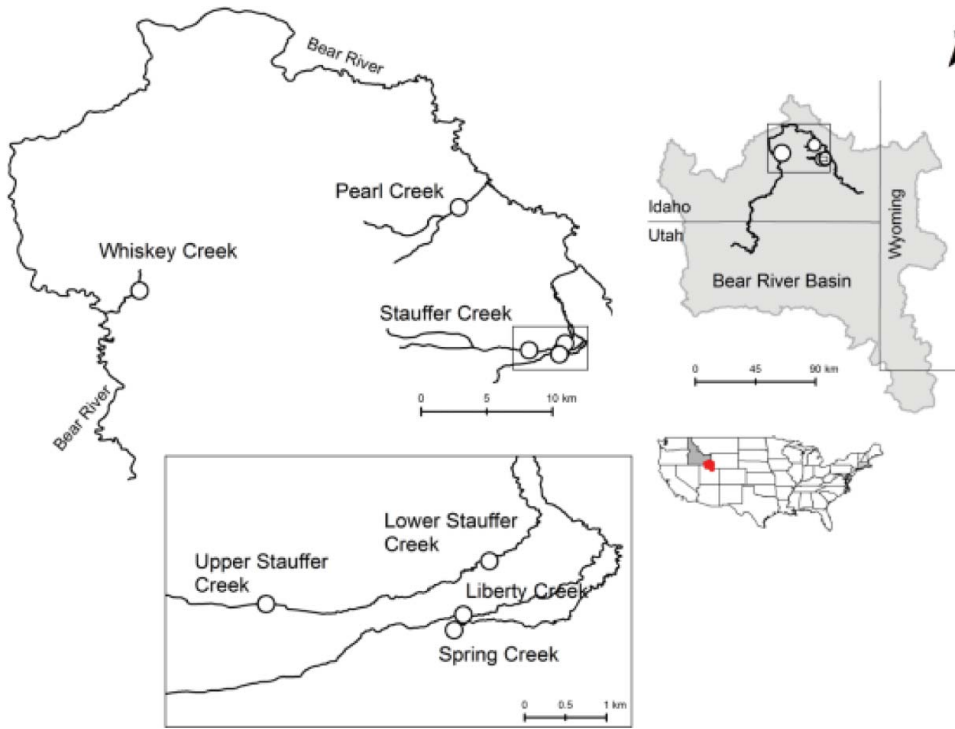*A 600-m reach was sampled in 2011, but only the downstream 200 m of this 600-m reach was sampled in 2013 and 2014.

Figure 1. Locations of the five study streams in the Bear River Basin of Idaho.

To estimate trout TBP, I followed methods detailed in Bellmore et al. (2013). I calculated the relative fraction of trout production attributed to aquatic or terrestrial prey (F_i) as

$$F_i = G_i \times AE_i \times NPE \quad (1)$$

where G_i is the proportion by mass of prey type i in a trout diet, AE_i is the assimilation efficiency of prey type i, and NPE is the net production efficiency. The proportion of trout production attributed to each prey type (PF_i) was then calculated from the relative fractions (F_i) as

$$PF_i = \frac{F_i}{\sum_{i=1}^{n} F_i} \quad (2)$$

As in Bellmore et al. (2013), I used the following assimilation efficiencies for cutthroat trout: 0.75 for aquatic invertebrates and 0.70 for terrestrial invertebrates. To be conservative, I also used an

Table 2. Description of fish diet, terrestrial invertebrate, and aquatic invertebrate data used in spring and snowmelt stream comparisons.

Stream	Sampling years	Fish diet samples (n)	Total length (mm; range)	Terrestrial pan traps, 2014 (n)	Benthic samples per year (n)
Spring	2011—2014	244	93—300	15	9
Liberty	2012—2014	30	112—340	–	3
Whiskey	2011	29	165—256	–	9
Upper Stauffer	2011—2014	279	80—304	15	9
Lower Stauffer	2011, 2013—2014	99	86—400	–	9
Pearl Creek	2012	32	81—187	–	3

average assimilation efficiency (0.725) for both prey types. Net production efficiency values were set at 0.125 for adult cutthroat ($\geq$150 mm) and 0.250 for juvenile cutthroat. Given that these values have not been validated for Bonneville cutthroat trout and that assimilation and production efficiencies vary with temperature, TBP estimates provide an initial means to compare trophic linkage importance across stream types.

Available aquatic prey

A variety of measures exist to describe the quality and quantity of food resources available to fish, including frequency of occurrence, biomass, energetics, and stoichiometry. Here, I used the biomass (i.e. prey weights) and abundance (i.e. prey counts) of benthic aquatic invertebrates to describe the quality and quantity of *in situ* resources (Evangelista et al. 2014). Prey weights provide information about the energetic importance of different prey types, without having to make untested assumptions about caloric content (e.g. joules g^{-1}). In addition, prey weights are more useful than prey counts because weights are measured in comparable units (Chipps & Garvey 2007). A limitation of using prey weights is that certain taxa with less digestible body parts, such as cased caddis flies or shelled snails, may be overrepresented.

Bonneville cutthroat trout consume primarily drifting invertebrates rather than benthic invertebrates (Hilderbrand & Kershner 2004), so invertebrate drift samples provide direct insight on *in situ* resource quality and quantity. However, few drift samples were collected, while benthic samples were collected with high intensity each year (Table 2). Benthic samples provide less information about the instantaneous biomass and abundance of drifting invertebrates, but benthic densities are related to cumulative drift densities collected over longer time periods (Allan 1987). Therefore, I used available data on the biomass and abundance of benthic aquatic invertebrates to describe the sustained availability of drifting invertebrates to trout.

Surber samples (90 s; 500 cm^2; mesh size 200 μm) were collected from randomly selected riffles at each stream site (Table 2). For each sample, Rhithron Associates counted the total number of invertebrates and then randomly selected 500 individuals to identify. Invertebrate weights were not recorded, so I used site- and year-specific weights of conspecifics from trout diet samples to estimate site- and year-specific weights of benthic invertebrates. Because I lacked data on invertebrate weights and lengths, I was not able to make inferences about trout size-selective foraging. When conspecifics did not occur in trout diet samples, I used site- and year-specific estimates of the mean individual prey weights for all individuals within the same taxonomic family or order. Benthic invertebrate weights and counts were summed for each sample and then scaled up to the total number of invertebrates in the sample. I used the mean of the summed benthic invertebrate weights and the mean of the summed counts for each site and year in analyses.

Terrestrial invertebrate inputs

I used existing data on terrestrial invertebrate inputs to test if consumption of terrestrial invertebrates was related to their availability. Terrestrial invertebrate input data were only available for Spring Creek and Upper Stauffer Creek in 2014 (Table 2). I placed 15 pan traps at equidistant locations within each 600-m reach, 29 July to 2 August 2014. Distance from the stream's wetted edge was randomized for each pan trap. Pan traps were plastic containers (15 $\times$ 30 cm) filled with approximately 3 cm of stream water. I added biodegradable soap to reduce water surface tension (Wipfli 1997; Saunders & Fausch 2007). Traps floated on the water's surface for 96 hr. Contents of traps were placed in plastic containers, preserved in 95% ethanol, and identified to the lowest practical level, and counted and weighed by Rhithron Associates (Missoula, MT). For each pan trap sample, I determined the total weight and abundance for only invertebrates that were terrestrial in origin.

Analyses

I used general linear mixed models (GLMMs) to compare trout consumption of aquatic and terrestrial invertebrates between spring and snowmelt streams. Diet weight (mg) and prey count from aquatic and terrestrial invertebrates were the response variable for the GLMMs. I standardized diet weights and prey counts by trout total length (mm^{-1}) since fish size (e.g. gape-width limitation and metabolic rate) can influence prey selection. Fixed factors were stream type (spring and snowmelt), prey source (aquatic and terrestrial), and stream type × prey source. Random factors were site, year, and individual. If the interaction of stream type × prey source was significant, I used contrasts to assess how trout diets differed by stream type and prey source. I also used GLMMs to evaluate differences in aquatic versus terrestrial TBP. The response variables were aquatic and terrestrial invertebrate PF_i, the fixed factor was stream type, and random factors were site and year. I was not able to test for an interaction of PF_i prey source with stream type since aquatic and terrestrial invertebrate PF_i were not independent of one another (i.e. $1 - PF_{aquatic} = PF_{terrestrial}$). I report mean PF_i as a range based on conservative AE_i parameters and the AE_i values used by Bellmore et al. (2013). I used analysis of variance to test if terrestrial inputs differed between Spring Creek and Upper Stauffer Creek. Terrestrial total weight and count data for each pan trap were log-transformed to satisfy assumptions of normality.

I also used GLMMs to test if the ratio of consumed terrestrial prey to consumed aquatic prey declined as the quality or quantity of *in situ* resources increased. I used the biomass of consumed prey and the biomass of available aquatic prey documented in benthic samples as surrogates for quality and I used the number of consumed prey and the number of available aquatic prey as surrogates for quantity. The response of the quality GLMM was the ratio of consumed terrestrial biomass (mg) to aquatic prey biomass (mg) and the response of the quantity GLMM was the ratio of the number of terrestrial prey consumed to the number of aquatic prey consumed. Fixed factors were stream type and available aquatic prey (mean of the summed benthic invertebrate weights for the quality GLMM and the mean of the summed benthic invertebrate counts for the quantity GLMM). Random factors were site and year.

Results

I analyzed the diets of 303 trout in spring streams and 410 trout in snowmelt streams (Table 2). In spring streams, 183 trout (60%) fed only on aquatic prey and 0 trout fed only on terrestrial prey. The dominant prey items by weight were amphipods and aquatic oligochaetes and the most abundant prey items were amphipods, aquatic oligochaetes, dipterans, and ephemeropterans. In snowmelt sites, 87 trout (21%) fed only on aquatic prey and 27 trout (7%) fed only on terrestrial prey. The dominant prey items by weight were terrestrial oligochaetes, which comprised 77%–100% of terrestrial prey weights when present in diets. The most abundant prey items were coleopterans, dipterans, hemipterans, and hymenopterans.

Trout diet composition by weight was a function of the interaction of stream type × prey source (Figure 2; $F_1 = 9.23$, $P < 0.01$). In spring streams, greater weights of aquatic prey were consumed than terrestrial prey ($F_1 = 3.70$, $P = 0.05$). In snowmelt streams, greater weights of terrestrial prey were consumed than aquatic prey ($F_1 = 5.88$, $P = 0.02$). When these data were re-analyzed without terrestrial oligochaetes, the contribution of aquatic prey to trout was further emphasized in spring streams ($F_1 = 7.75$, $P < 0.01$) but did not differ from terrestrial prey in snowmelt streams ($F_1 = 0.03$, $P = 0.86$). Prey count was also a function of stream type × prey source (Figure 2; $F_1 = 210.03$, $P < 0.01$). Trout in both stream types consumed more aquatic than terrestrial prey ($F_1 = 360.21$, $P < 0.01$). Trout in spring streams consumed more aquatic prey than trout in snowmelt streams ($F_1 = 37.30$, $P < 0.01$), while trout consumed more terrestrial prey in snowmelt streams than in spring streams ($F_1 = 7.02$, $P = 0.05$). Random effects comprised less than 6% and 4% of the total variance in the diet weight and prey count models, respectively, which indicates that consumption patterns were consistent among individuals, sites and years within each stream type.
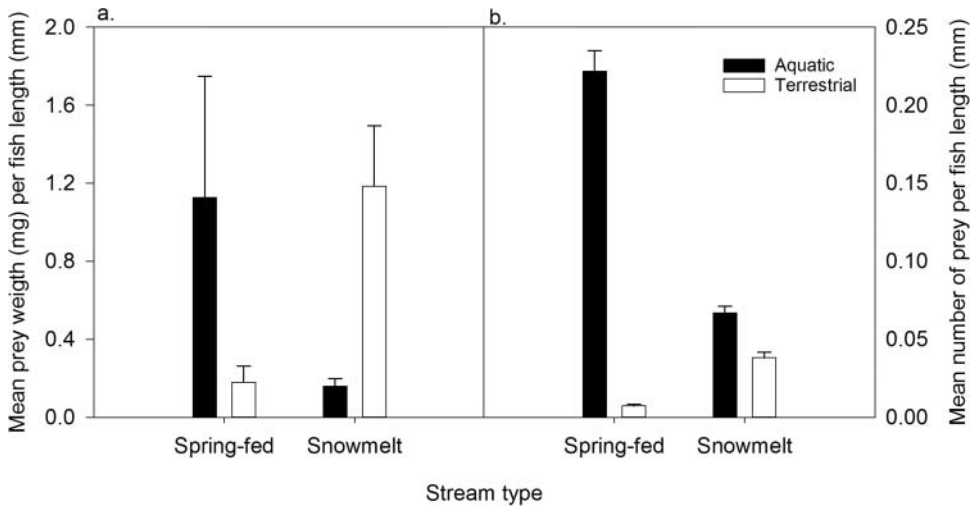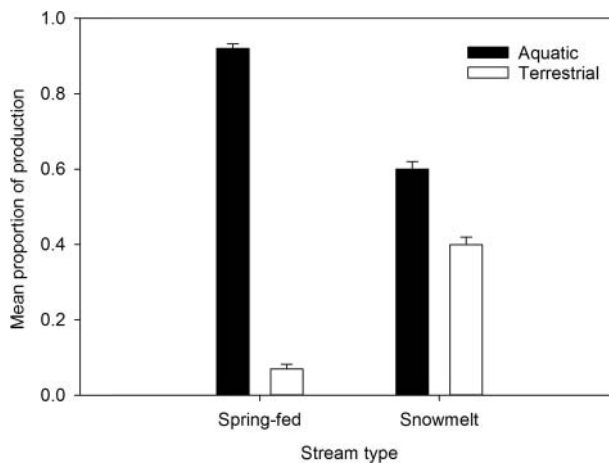
Figure 2. The (a) mean (±1 SE) weight and (b) mean (±1 SE) number of aquatic (filled bars) and terrestrial (unfilled bars) prey consumed by trout in spring-fed and snowmelt-dominated streams. Prey weights and number are standardized by fish length (mm).

Nearly 83%–93% (1 SE ± 0.9%–1.2%) of trout production in spring streams and 60%–66% (± 0.09%–2.0%) in snowmelt streams were fueled by aquatic invertebrates, while the remainder of trout production in each stream type was from terrestrial production (Figure 3). However, differences in the aquatic trophic TBP and terrestrial TBP between stream types were not significant due to high variation among snowmelt stream sites ($F_1 = 1.87$, $P = 0.24$).
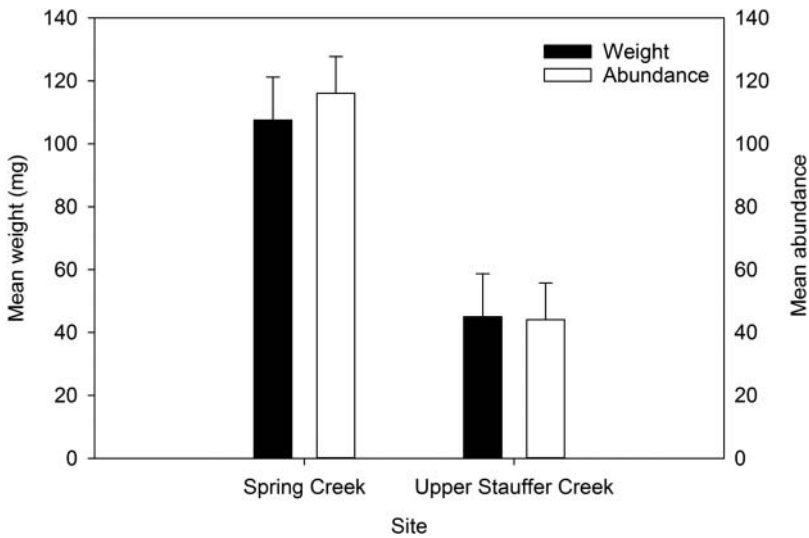
Terrestrial invertebrate inputs to Spring Creek were greater than Upper Stauffer Creek (Figure 4). The total weight and count of terrestrial invertebrates found in pan traps were greater in Spring Creek ($F_{28} = 15.11$, $P < 0.01$ and $F_{28} = 21.93$, $P < 0.01$, respectively). Terrestrial oligochaetes were not documented in pan traps or in benthic samples.

Biomass and count ratios of consumed terrestrial and aquatic prey were not related to the quality or quantity of benthic macroinvertebrates (Figure 5). Analyses without terrestrial oligochaetes did not change results. Spring sites had little variation in terrestrial to aquatic weight and abundance ratios ($\sigma^2 < 0.50$ with and without terrestrial oligochaetes), despite considerable variation in available benthic invertebrate weight and abundance ($\sigma^2 > 5.68 \times 10^5$). Snowmelt sites had greater

Figure 3. The mean (±1 SE) proportion of production attributed to aquatic (filled bars) and terrestrial (unfilled bars) invertebrates in spring-fed and snowmelt-dominated streams.

Figure 4. The mean (±1 SE) weight (filled bars) and abundance (unfilled bars) of terrestrial invertebrate inputs into the spring-fed Spring Creek and the snowmelt-dominated Upper Stauffer Creek in July 2014.

variation in terrestrial to aquatic weight ($\sigma^2 = 24.99$ with terrestrial oligochaetes, $\sigma^2 = 2.42$ without terrestrial oligochaetes) but low variation in abundance ratios ($\sigma^2 < 0.50$ with and without terrestrial oligochaetes), and these ratios did not track available benthic invertebrate weight and abundance. Consequently, weight and abundance ratios did not vary by stream type ($F_1 > 2.35$, $P > 0.27$) or benthic invertebrate biomass ($F_1 < 0.62$, $P > 0.45$). The random factor of site comprised 57% and 37% of the total variation in the biomass and count ratios, respectively, while year comprised ~0% of the variation for both response variables.

Discussion

Multiple lines of evidence over the past 30 years indicate that aquatic consumers can be highly dependent upon terrestrial subsidies (e.g. Kawaguchi et al. 2003). In this study, I demonstrated considerable variation in trout consumption of terrestrial subsidies within high-altitude desert streams and this variation was related to stream type rather than *in situ* resource availability. I found that aquatic and terrestrial invertebrates both contributed to trout TBP in spring and snowmelt streams, though the importance of aquatic invertebrates relative to terrestrial invertebrates was much greater in spring streams. Terrestrial invertebrate inputs were greater in spring streams, yet terrestrial invertebrates, especially oligochaetes, made larger contributions to trout TBP and diets in snowmelt streams. From these data, I can infer that local processes have a strong influence on trout energetics in spring streams, while processes that influence trout energetics in snowmelt streams extend beyond the local system. Comparison of our results to those found in forested north temperate systems, where terrestrial invertebrates comprise a large proportion of the annual energy budgets of trout (Nakano et al. 1999; Baxter et al. 2004), suggests that there are limits to generalizations about trophic linkages. The spatial variation in trophic linkages that I documented within and among stream types complicates management, but awareness of this variation is critical for developing effective trout conservation strategies.

The causes of variation in the importance of aquatic–terrestrial trophic linkages remain unclear. Contrary to my prediction, the biomass and occurrence of consumed terrestrial and aquatic prey were not related to the quality or quantity of *in situ* resources (Figure 4); where quality and quantity were defined as benthic invertebrate biomass and relative abundance, respectively. Spring and
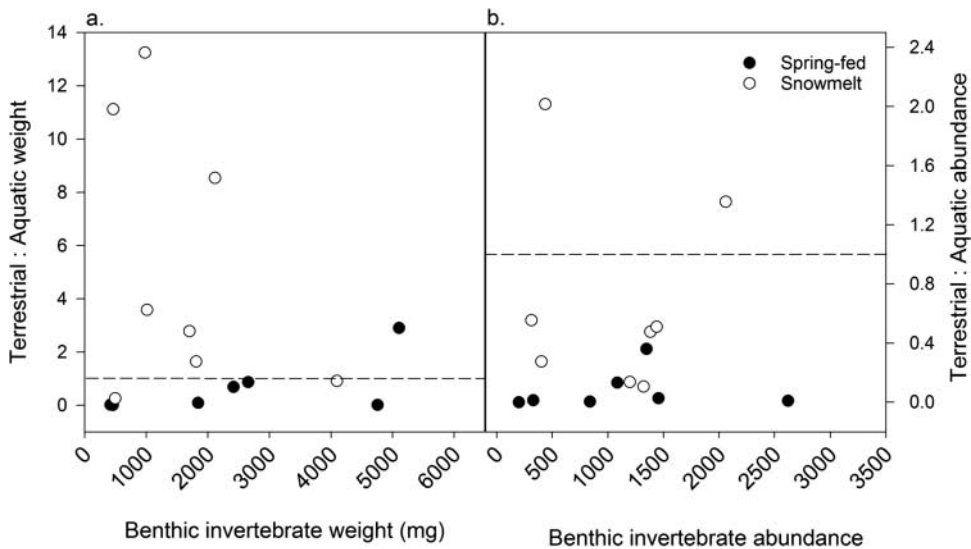
Figure 5. The ratios of (a) consumed terrestrial to aquatic prey weight vs. available benthic invertebrate weight and (b) consumed terrestrial to aquatic prey abundance vs. available benthic invertebrate abundance in spring-fed (filled circles) and snowmelt-dominated (unfilled circles) streams. The dashed lines indicate a consumed terrestrial to aquatic prey ratio of 1:1.

snowmelt streams had comparable *in situ* resources (i.e. similar values of benthic invertebrate weights and abundance), yet trout consumption patterns were distinct between these stream types. For trout in spring streams, the ratio of consumed terrestrial to aquatic prey was invariant and always <1, despite a fivefold difference in available benthic invertebrate resources (Figure 5). For trout in snowmelt streams, the ratio of consumed terrestrial to aquatic prey was more variable among sites, even when benthic invertebrate resources were relatively scarce (Figure 5). Integrating our results with drift net samples and stoichiometry to better quantify *in situ* resources, collecting additional diet samples throughout the year to assess seasonal differences in trophic linkage strength, and using stable isotopes to reflect longer term foraging strategies may help clarify the documented variation.

An alternative to the *in situ* hypothesis is that the stability of spring streams may allow trout to specialize on aquatic prey, regardless of the quality or quantity of *in situ* and terrestrial prey. In general, spring streams exhibit more dampened seasonal and annual variation in temperature, flow, and chemistry than snowmelt streams. This stability can result in net autotrophic systems with abundant ambient resources (Minshall 1978; Cushing & Wolf 1984; Barquín & Death 2006; Godwin & Carrick 2008); in this study, the highest values of *in situ* resource quality and quantity were in spring streams (Figure 5). This stability was also reflected in trout diets and benthic invertebrate composition, as amphipods (*Gammarus* spp.) consistently dominated diet and benthic samples by weight and number in spring streams while dominant taxa by number temporally and spatially varied in snowmelt streams. Notably, amphipods were absent in trout diets and benthic samples in snowmelt streams. Amphipods have been recognized as an important food source for fish because they are present year round, abundant, and large in size (Macneil et al. 1999; Laudon et al. 2005). However, they can have a lower energy density than terrestrial invertebrates (Cummins & Wuycheck 1967). The stability of spring streams may allow trout to have a high encounter rate with and become efficient at capturing, handling, and consuming amphipods and other aquatic prey. Foraging and assimilation efficiency can be an important component of resource quality (Wipfli & Baxter 2010). Thus, specialization on an abundant, stable prey source may trump the benefits of consuming terrestrial prey. Indeed, brown trout (*Salmo trutta*) that specialized on aquatic predator invertebrates had higher growth rates than brown trout that also consumed terrestrial invertebrates

(Evangelista et al. 2014). Specialization, rather than opportunism, has been observed in multiple fish species (Beaudoin et al. 1999; Grey 2001), but it usually occurs among individuals rather than at the population level that I documented (Evangelista et al. 2014).

An important result in our study is that certain prey taxa can contribute disproportionately to the importance of trophic linkages between aquatic and terrestrial ecosystems. Consumption of amphipods increased the relative importance of aquatic resources in spring streams, while consumption of terrestrial oligochaetes (e.g. earthworms) increased the importance of terrestrial inputs in snowmelt streams. I documented 59 terrestrial oligochaetes in 45 of 410 trout diets in snowmelt streams. Most trout only consumed one oligochaete, but the oligochaete's large size had a disproportionate effect on diet prey weights. Individual weights ranged from 0.009 to 5.500 g, whereas the median prey weight of all other individuals was 0.001 g. When terrestrial oligochaetes were excluded from analyses, the relative importance of terrestrial and aquatic prey to trout was similar in snowmelt streams. Consequently, factors that influence terrestrial oligochaete inputs into streams are likely to be important to trout energetics. The presence of terrestrial oligochaetes in trout diets has been associated with rain events (e.g. Allan 1981), though I only observed rain on one sample day over this four-year study and rain is likely to occur at all of sites given their relatively close location (Figure 1). Alternatively, the supply of terrestrial invertebrates into streams can be different for different riparian vegetation types (Kautza & Sullivan 2014; Kawaguchi & Nakano 2001). Riparian vegetation type differed across our study streams; shrubs and herbaceous plants were the dominant land cover for spring streams while open forests were the dominant land cover for snowmelt streams. However, little is known about how riparian vegetation type influences the identity (i.e. taxa) of terrestrial inputs. Terrestrial oligochaetes did occur in spring streams, as I documented this prey item in 10 trout. However, I do not know if inputs differed between stream types since terrestrial oligochaetes were not observed in pan traps and benthic samples (*this study*) or multiple drift samples (*unpublished data*).

The variation in trophic linkage importance between aquatic and terrestrial ecosystems documented in this study underscores the importance of spring streams to trout conservation in a changing climate. Because trout diets in spring streams had a weaker link to terrestrial ecosystems, trout in spring streams may be more robust to climate-induced impacts on the timing or quantity of terrestrial invertebrate fluxes than trout in snowmelt streams. In addition, spring streams have buffered water temperatures and dampened flows, so climate impacts on instream productivity should occur at a slower rate than in snowmelt streams (Durance & Ormerod 2007). A conservation portfolio that allows for a diversity of trophic pathways may be critical for long-term conservation of trout, but a better understanding of what drives spatial variation in trophic linkage importance is still needed for informed management of stream fish populations.

Disclosure statement

The author declares no competing financial interests or benefits exist.

Notes on contributor

Adam Sepulveda is a Research Zoologist with the U.S. Geological Survey, Northern Rocky Mountain Science Center in Bozeman, Montana, USA. His research focuses on aquatic invasive species issues and food webs in flowing waters of the western United States.

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References

Allan JD. 1981. Determinants of diet of brook trout (*Salvelinus fontinalis*) in a mountain stream. Can J Fish Aquat Sci. 38:184–192.

Allan JD. 1987. Macroinvertebrate drift in a Rocky Mountain stream. Hydrobiologia. 144:261–268.

Barquín J, Death RG. 2006. Spatial patterns of macroinvertebrate diversity in New Zealand springbrooks and rhithral streams. J North Am Benthol Soc. 25:768–786.

Barrow LM, Bjorndal KA, Reich KJ. 2008. Effects of preservation method on stable carbon and nitrogen isotope values. Physiol Biochem Zool. 81:688–693.

Baxter CV, Fausch KD, Carl S. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshw Biol. 50:201–220.

Baxter CV, Fausch KD, Murakami M, Chapman PL. 2004. Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. Ecology. 85:2656–2663.

Beaudoin CP, Tonn WM, Prepas EE, Wassenaar LI. 1999. Individual specialization and trophic adaptability of northern pike (*Esox lucius*): an isotope and dietary analysis. Oecologia. 120:386–396.

Bellmore JR, Baxter CV, Martens K, Connolly PJ. 2013. The floodplain food web mosaic: a study of its importance to salmon and steelhead with implications for their recovery. Ecol Appl. 23:189–207.

Boulton AJ, Datry T, Kasahara T, Mutz M, Stanford JA. 2010. Ecology and management of the hyporheic zone: stream-groundwater interactions of running waters and their floodplains. J North Am Benthol Soc. 29:26–40.

Chipps SR, Garvey JE. 2007. Analysis and interpretation of freshwater fisheries data. Bethesda, MD: American Fisheries Society. Chapter 11, Quantitative assessment of food habits and feeding patterns; p. 473–514.

Courtwright J, May CL. 2013. Importance of terrestrial subsidies for native brook trout in Appalachian intermittent streams. Freshw Biol. 58:2423–2438.

Cummins KW, Wuycheck JC. 1967. Calorific equivalents for studies in ecological energetics. Int Assoc Theor Appl Limnol. 18:158.

Cushing C, Wolf E. 1984. Primary production in Rattlesnake Springs, a cold desert spring-stream. Hydrobiologia. 114:229–236.

Durance I, Ormerod SJ. 2007. Climate change effects on upland stream macroinvertebrates over a 25–year period. Glob Chang Biol. 13:942–957.

Evangelista C, Boiche A, Lecerf A, Cucherousset J. 2014. Ecological opportunities and intraspecific competition alter trophic niche specialization in an opportunistic stream predator. J Anim Ecol. 83:1025–1034.

Godwin CM, Carrick HJ. 2008. Spatio-temporal variation of periphyton biomass and accumulation in a temperate spring-fed stream. Aquat Ecol. 42:583–595.

Grey J. 2001. Ontogeny and dietary specialization in brown trout (*Salmo trutta* L.) from Loch Ness, Scotland, examined using stable isotopes of carbon and nitrogen. Ecol Freshw Fish. 10:168–176.

Griffith J. Jr 1974. Utilization of invertebrate drift by brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Salmo clarki*) in small streams in Idaho. Trans Am Fish Soc. 103:440–447.

Hilderbrand RH, Kershner JL. 2004. Influence of habitat type on food supply, selectivity, and diet overlap of Bonneville cutthroat trout and nonnative brook trout in Beaver Creek, Idaho. N Am J Fish Manag. 24:33–40.

Junk WJ, Bayley PB, Sparks RE. 1989. The flood pulse concept in river-floodplain systems. Can Spec Publ Fish Aquat Sci. 106:110–127.

Kautza A, Sullivan SMP. 2014. Shifts in reciprocal river-riparian arthropod fluxes along an urban–rural landscape gradient. Freshw Biol. 60:2156–2168.

Kawaguchi Y, Nakano S. 2001. Contribution of terrestrial invertebrates to the annual resource budget for salmonids in forest and grassland reaches of a headwater stream. Freshw Biol. 46:303–316.

Kawaguchi Y, Taniguchi Y, Nakano S. 2003. Terrestrial invertebrate inputs determine the local abundance of stream fishes in a forested stream. Ecology. 84:701–708.

Laudon MC, Vondracek B, Zimmerman JK. 2005. Prey selection by trout in a spring-fed stream: terrestrial versus aquatic invertebrates. J Freshw Ecol. 20:723–733.

Macneil C, Dick JT, Elwood RW. 1999. The dynamics of predation on Gammarus spp.(Crustacea: Amphipoda). Biol Rev. 74:375–395.

Marcarelli AM, Baxter CV, Mineau MM, Hall RO. Jr 2011. Quantity and quality: unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. Ecology. 92:1215–1225.

Marczak LB, Thompson RM, Richardson JS. 2007. Meta-analysis: trophic level, habitat, and productivity shape the food web effects of resource subsidies. Ecology. 88:140–148.

Minshall GW. 1978. Autotrophy in stream ecosystems. Bioscience. 28:767–771.

Minshall GW, Cummins KW, Petersen RC, Cushing CE, Bruns DA, Sedell JR, Vannote RL. 1985. Developments in stream ecosystem theory. Can J Fish Aquat Sci. 42:1045–1055.

Nakano S, Kawaguchi Y, Taniguchi Y, Miyasaka H, Shibata Y, Urabe H, Kuhara N. 1999. Selective foraging on terrestrial invertebrates by rainbow trout in a forested headwater stream in northern Japan. Ecol Res. 14:351–360.

Nakano S, Miyasaka H, Kuhara N. 1999. Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. Ecology. 80:2435–2441.

Resh VH, Brown AV, Covich AP, Gurtz ME, Li HW, Minshall GW, Reice SR, Sheldon AL, Wallace JB, Wissmar RC. 1988. The role of disturbance in stream ecology. J North Am Benthol Soc. 7:433–455.

Robinson C, Minshall G. 1998. Macroinvertebrate communities, secondary production, and life history patterns in two adjacent streams in Idaho, USA. Archiv Hydrobiol. 142:257–281.

Saunders WC, Fausch KD. 2007. Improved grazing management increases terrestrial invertebrate inputs that feed trout in Wyoming rangeland streams. Trans Am Fish Soc. 136:1216–1230.

Sepulveda AJ, Layhee M, Sutphin ZA, Sechrist JD. 2015. Evaluation of a Fine Sediment Removal Tool in Spring-fed and Snowmelt Driven Streams. Ecol Restor. 33:303–315.

Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE. 1980. The river continuum concept. Can J Fish Aquat Sci. 37:130–137.

William D, Hynes H. 1974. The occurrence of benthos deep in the substratum of a stream. Freshw Biol. 4:233–256.

Williams JE, Haak AL, Neville HM, Colyer WT. 2009. Potential consequences of climate change to persistence of cutthroat trout populations. N Am J Fish Manag. 29:533–548.

Wilson MK, Lowe WH, Nislow KH. 2014. What predicts the use by brook trout (Salvelinus fontinalis) of terrestrial invertebrate subsidies in headwater streams? Freshw Biol. 59:187–199.

Winterbourn MJ, Rounick J, Cowie B. 1981. Are New Zealand stream ecosystems really different? N Z J Mar Freshw Res. 15:321–328.

Wipfli MS. 1997. Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: contrasting old-growth and young-growth riparian forests in southeastern Alaska, USA. Can J Fish Aquat Sci. 54:1259–1269.

Wipfli MS, Baxter CV. 2010. Linking ecosystems, food webs, and fish production: subsidies in salmonid watersheds. Fisheries. 35:373–387.