

THESIS

RECIPROCAL SUBSIDIES IN A FOURTH ORDER ROCKY MOUNTAIN STREAM

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ABSTRACT

RECIPROCAL SUBSIDIES IN A FOURTH ORDER ROCKY MOUNTAIN STREAM

Subsidies are defined as nutrients, energy, or resources that cross arbitrarily defined boundaries from one system to another. Streams have long been viewed as being dependent on terrestrial subsidy inputs, mostly in the form of leaf litter, to form the base of the food web. More recently, however, the importance of terrestrial invertebrate inputs to trout has been noted. Additionally, emerging aquatic insects have been shown to be a reciprocal subsidy to riparian insectivores (Baxter et al. 2005).

I examined these reciprocal subsidies in the Upper Arkansas River Basin, near Leadville, Colorado, USA. The Arkansas River at this location is a fourth order stream at approximately 2,820 msl (meters above sea level). It is characterized by a short growing season, with average annual high and low temperatures of 9.6 and -6.4°C, respectively, and receives an average annual precipitation of 29.5 cm, primarily as snow in the winter. The Upper Arkansas River was subjected to extensive mining activities beginning in the mid 19th century. Chemical remediation began in the early 1990's, and metal levels have been near or below criterion levels set by the Environmental Protection Agency (EPA) to protect 95% of aquatic life since the early 2000's (Clements et al 2010). Although some legacy effects of heavy metal contamination remain, benthic insect abundances and species richness have largely recovered and are similar to unpolluted Colorado streams. In addition to heavy metal contamination, the riparian zone was historically impacted from grazing. Grazers were removed, and some riparian re-vegetation occurred in 1999. The riparian zone has improved, with homogenous patches of willows, grasses, and gravel bars distributed throughout.

Although water quality has largely improved, physical in-stream habitat improvements took place in the fall of 2013, primarily to restore a brown trout (*Salmo trutta*) fishery. The present study was initiated as a baseline monitoring program to assess the effectiveness of these

restoration activities. Seven sites were located along a 4 km reach within the restoration area, approximately 13 km downstream from the town of Leadville, CO. Monitoring will continue for an additional 2 years, and the effectiveness of the restoration will be presented at that time.

Chapter 1 assesses the importance of terrestrial invertebrates falling into the stream for brown trout. Previous work has indicated that terrestrial invertebrates provide an important energy subsidy to salmonids, but most of this work was conducted on small, headwater streams (order 1-3) in the North Temperate Zone, generally with dense riparian vegetation, and a relatively closed canopy. The importance of terrestrial invertebrate inputs to trout in larger streams remains unknown. Additionally, to my knowledge, these subsidies have never been examined in a restoration context.

In addition to assessing the relative importance of terrestrial invertebrates to the restoration reach, I examined the small-scale differences of terrestrial inputs based on riparian vegetation. The patchy, homogenous, riparian vegetation along the Upper Arkansas River Basin is an ideal system to examine the influence on habitat type on terrestrial subsidies to the stream. I placed pan traps under three habitat categories, willow, grass, and gravel, at six sites twice annually in August in 2012 and 2013. All invertebrates were identified and dried to assess dry mass. Terrestrial invertebrate inputs were similar between years, and were significantly greater in the vegetated (grass and willow categories) versus the un-vegetated gravel bars. Pan traps placed in gravel habitats received an average of 6.7 mg of terrestrial invertebrate input per $m^{-2} * d^{-1}$ (dry mass), compared to an average of 39.2 and 42.6 mg per $m^{-2} * d^{-1}$ in the willow and grass habitats, respectively.

In order to assess the relative importance of these terrestrial invertebrates to trout diets, I sampled approximately 80 brown trout stomachs via gastric lavage in both years. All invertebrates were identified to the lowest practical level, and were dried in order to assess dry mass. There was significant annual variation, but trout that consumed terrestrial invertebrates had total stomach

contents that weighed approximately twice as much as fish that only consumed aquatic invertebrates. Interestingly, trout consumed more terrestrial invertebrates in 2013 than 2012, despite having approximately equivalent inputs in both years. The availability of aquatic invertebrates, however, was significantly greater in 2013 than in 2012. It appears that the increase in availability of aquatic prey elicited an increased foraging response in trout, and an incidental increase in terrestrial invertebrate consumption.

These results highlight the importance of maintaining terrestrial-aquatic linkages by maintaining a healthy riparian zone. Management practices that encourage riparian growth, such as excluding grazers from riparian zones, utilization of willow plantings and other “green” engineering techniques for bank stabilization, will strengthen these connections, and provide a valuable resource to the local fishery. Additionally, I propose emphasizing riparian remediation in river restoration projects as an important goal and objective. It appears that if you “build a healthy riparian zone, the invertebrates will come.”

Chapter 2 assesses the reciprocal aquatic subsidy export to the riparian zone. I sampled benthic invertebrate communities, emerging aquatic insects, and subsequent return of adults to the water surface in order to estimate the net flux of aquatic invertebrates to the riparian zone, using a mass balance approach. Five replicate Hess samples (0.1m² area) were taken from four sites along the Upper Arkansas River Basin. Three floating emergence traps (0.33m² area) were deployed for 48 hour intervals twice yearly, at six sites along the restoration reach. Aquatic invertebrate input was assessed using pan traps deployed simultaneously as the emergence traps (Chapter 1). Sampling was conducted annually in August from 2010-2013. All invertebrates were identified to the lowest practical taxonomical unit, and dry mass was assessed from all samples in 2012 and 2013.

There was no spatial variation in samples, but there was significant annual variation. Benthic, emergence, and aquatic input biomass were all significantly greater in 2013 than in 2012. I

estimated that 25.7 and 67.3 mg dry mass were exported to the riparian zone per $m^{-2} * d^{-1}$ in 2012 and 2013, respectively. This demonstrates that there can be significant annual variation in cross-ecosystem subsidies. It is likely that these differences were related to annual variation in the hydrologic regime, as 2012 was an extremely dry year and 2013 showed a significant increase in annual discharge. These findings highlight the importance of conducting ecological studies for more than one year in order to characterize the natural range of variability. In addition, this study shows the importance of measuring multiple endpoints in food web studies. For example, a majority of studies examining aquatic subsidy export only collect emerging adults, and assume that a majority (generally >90%) is exported to the riparian zone. In the present study, I found that 70% and 50% of all emergent biomass was exported to the riparian zone in 2012 and 2013, respectively. The estimated magnitude of aquatic export would be significantly greater if I assumed that 90% of all emergent biomass was exported

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Chapter 1: Terrestrial Subsidy Availability And Utilization By Brown Trout In A Fourth Order Rocky Mountain Stream

Introduction

Ecosystems have been historically viewed as self-contained with their internal dynamics being more important than outside forces (Forbes 1887). The lateral boundaries of these systems were usually defined arbitrarily, often for the sake of convenience. Recent work has shown the importance of fluxes of materials and energy across these 'boundaries', particularly in spatially coupled ecosystems (Richardson and Sato 2014). Polis et al. (1997) defined subsidies as passive, donor-controlled resources that cross the boundary from one system to another, and increases the productivity of the recipient community. In the past few decades, the importance of these linkages between systems has received much attention. These linkages can also have important effects on recipient communities, influencing population dynamics, behavior, and trophic cascades (Baxter et al. 2005).

Streams and their associated riparian areas are an often studied example of this phenomenon. The importance of leaf litter entering streams has been a defining characteristic of lotic ecology, particularly in low order North Temperate streams, for many decades (Vannote et al. 1980). The River Continuum Concept (RCC) hypothesized that low order streams would have low primary productivity and would rely on a majority of their nutrients and energy coming from leaf litter falling into streams. These materials are the base of the food chain, and become available to higher trophic levels indirectly, through algae, aquatic plants, and stream invertebrates. More recently, it has been shown that terrestrial invertebrates falling into streams are a resource subsidy directly available to fish (Mason and MacDonald 1982), particularly Salmonidae (see Baxter et al. 2005 for a review).

These terrestrial invertebrate subsidies may provide up to 50% of annual energy requirements for salmonids, even though they are typically only available for a few months out of the year (Nakano *et al.* 1999b; (Kawaguchi and Nakano 2001). Estimates of terrestrial inputs in summer range from as little as 1.3 mg m⁻² day⁻¹ dry mass to as high as 450 mg m⁻² day⁻¹ dry mass (Baxter *et al.* 2005) and from 1 individual (Edwards and Huryn 1995) to >200 individuals per m⁻² d⁻¹ (Cloe and Garman 1996). Terrestrial inputs have been shown to be affected by land use (Edwards and Huryn 1995, 1996, Saunders and Fausch 2007, 2012), dominant vegetation type (Wipfli 1997, Kawaguchi and Nakano 2001, Allan *et al.* 2003) and stream order (Cloe and Garman 1996).

Terrestrial invertebrate subsidy availability generally peaks between late spring and early autumn, when the riparian zone has maximum productivity (Kawaguchi and Nakano 2001). The timing of this peak is particularly important to fish because of the reduced availability of benthic invertebrates in summer and autumn (Hynes 1970; (Nakano and Murakami 2001). Many aquatic insects display synchronized emergences from spring through summer, thereby reducing the benthic prey availability. The input of terrestrial invertebrates into streams may partially answer “Allen’s Paradox”, which was based on his 1951 observation that a New Zealand stream did not have sufficient secondary productivity to support the fish population.

Numerous studies have shown that salmonids preferentially select terrestrial invertebrates, which may comprise 72.3%, by weight, of rainbow trout diets in some streams (Nakano *et al.* 1999b). Another field study examining rainbow trout, dolly varden and white-spotted char, found that terrestrial invertebrates comprised ≥ 50% of their diets in summer (Nakano *et al.* 1999a). Likewise, Bridcut (2000) found that terrestrial and adult aquatic insects comprised 86% of brown trout diets in an English stream. This may be due to the fact that terrestrial invertebrates are generally large, buoyant, usually more available during daylight hours, and highly visible against

the light sky, as well as a highly nutritious food item directly available to fish (Mason and MacDonald 1982).

Riparian vegetation is likely to influence the flux of terrestrial invertebrates to streams. Southwood (1961) noted that deciduous trees generally have more species and higher abundances of associated invertebrates than do coniferous trees. Mason and Macdonlad (1982) showed that some riparian tree species provided more terrestrial invertebrate mass to English streams. Edwards and Huryn (1995; 1996) examined terrestrial invertebrate inputs in a New Zealand trout stream, and found that they were higher in forested catchments and native grass pastures than in exotic grass pastures. Kawaguchi and Nakano (2001) sampled annual terrestrial inputs in a forested and grassland reach, and found inputs were similar at all times except in summer, when the forested reach contributed 1.7 times the biomass of the grassland reach. They also showed that overhanging vegetation increases terrestrial inputs. Wipfli (1997) showed that red-alder dominated canopies provide higher terrestrial inputs than conifer dominated canopies, although this finding was not significant. Likewise, Allan et al. (2003) examined terrestrial inputs along a gradient of red-alder to conifer dominated canopies, and found evidence that terrestrial inputs were higher in the red-alder dominated canopies than the conifer dominated canopies. The authors report that this finding was not significant, but that these small scale differences may be difficult to detect along a gradient of red-alder to conifer canopies.

Trees have a more complicated 3-D architecture than grass, provide more surface area for insects to occupy, and generally have more area overhanging the stream surface. Deciduous trees in particular generally have higher species richness and total abundance of insects; however, grasslands can provide similar abundances of insects, as well as support larger taxa such as Orthopterans due to their higher nutrient content (Edwards and Huryn 1995, Jonas and Joern 2008).

Most of the work examining linkages between aquatic and riparian systems has been conducted on low order, headwater streams in the North Temperate Zone (Baxter et al. 2005, Saunders and Fausch 2007, 2012). Cloe & Garman (1996), examined terrestrial inputs across a gradient of stream orders (2, 3, and 6), and found that mass and numbers of terrestrial invertebrates were greater at the second order site than the sixth. This is likely due to the increased width to edge ratio of larger streams, and the reduced amount of vegetation directly overhanging the stream (Polis et al. 1997, Kawaguchi and Nakano 2001, Richardson et al. 2010). Despite this study, our knowledge of terrestrial invertebrate inputs into mid-order streams remains minimal, particularly for salmonid bearing streams.

The Upper Arkansas River Basin is located in the mineralized belt of the Rocky Mountains, near Leadville, Colorado, USA. The area was the scene of significant mining activities from the mid 1800's through the late 20th century. As a result of these mining activities, particularly along California Gulch, a tributary to the Arkansas, water quality was severely reduced, and the native fishery was eradicated. The area was designated an EPA Superfund Site in 1983, and contaminant remediation and habitat restoration continues at the site. Chemical restoration took place in the early 1990's, and water quality is improving (Clements et al. 2010). Physical in-stream and riparian area restoration was initiated in the fall of 2013, and this study was initiated in 2012 as a baseline monitoring program to assess the effectiveness of this restoration. The goal of this restoration is to improve in-stream habitat for brown trout in order to improve the recreational fishery in this stream. Monitoring will continue for another 2 years, and the results of the restoration effectiveness will be presented at that time.

Vegetation type has been implicated in differences in terrestrial inputs into streams, but previous studies have been inconclusive. In addition to collecting samples for the baseline monitoring, I wanted to examine the small-scale differences in terrestrial invertebrate input based

on vegetation categories. The distribution of riparian vegetation along the restoration reach is patchy, with relatively homogenous habitats of grass, willows, and gravel bars, with some sparsely distributed alders, making this an ideal system to examine the small scale differences in inputs. The primary objective of this research was to determine the differences in abundance and biomass inputs of terrestrial insects from broadly defined riparian habitat categories, and the relative importance of terrestrial invertebrates to brown trout diets. In order to determine the relative importance of terrestrial invertebrates, I also sampled benthic community abundance and aquatic insect emergence and subsequent return inputs in order to estimate all prey resource availabilities to brown trout.

I hypothesized that 1) willows would have the greatest abundance of terrestrial insects falling into streams due to their large surface area and complex 3-D architecture; 2) grass areas would have similar abundances, but higher dry mass of terrestrial insects due to the presence of large taxa such as Orthopterans; and 3) gravel bars would have the lowest abundances, and dry mass of terrestrial insects due to reduced food and habitat availability. Additionally, I hypothesized that terrestrial invertebrates will be an important prey resource to brown trout in this system, as has been found in previous studies.

Methods

Study Site

Seven study sites (AR4.C, AR4.D, AR4.E, AR4.F, AR4.G, AR4.H and AR5) were located along a 4 km reach of the Upper Arkansas River Basin, near Leadville, Colorado, USA (Table 1.1). These sites were located immediately downstream from the historical source of metals to the river, and included one site (AR5) that has been sampled since 1989 (Clements *et al.* 2010). This area is located at approximately 2,820 msl (meters above sea level), has an average annual temperature of 9.6 and -6.4°C, and receives an average precipitation of 29.5 cm, mostly in the form of snow during

the winter. All sites had a substrate of predominantly medium to large cobble in a matrix of gravel and sand. The United States Geological Survey (USGS) operates a stream gauge between the two upstream sites (USGS gauge 07083710). No major tributaries enter the Arkansas River between this gauge and the most downstream site, so this information was used for stream discharge information. The Arkansas River is heavily regulated, with reservoirs upstream receiving trans basin diversions, and releasing water for agricultural, and municipalities. Despite this, the Arkansas River has a hydrograph typical of a snowmelt fed stream. The riparian corridor along this reach is primarily grass with dense, homogenous patches of willow distributed throughout, and large gravel bars on the inside of meander bends.

Invertebrate Sampling

Benthic macroinvertebrates were collected from 4 sites (AR4.D, AR4.F, AR4.G and AR5) in mid August in 2012 and 2013. Five replicates were collected from riffle habitats using a 0.1 m² Hess sampler (Clements et al 2010). Although fish forage in all riverine habitats, riffles are the standard habitat sampled for biological assessment of river health and generally support the highest invertebrate densities. Samples were placed in 80% ethanol and transported to Colorado State University. Samples were sorted in the lab, and then sent to Timberline Aquatics, Fort Collins, Colorado, for identification to the lowest practical level, generally species. After identification, these samples were archived in the Clements lab (Colorado State University, Fort Collins, Colorado), so they were not dried in order to estimate dry weight.

Aquatic insect emergence was assessed using 3 floating emergence traps at six sites (AR4.C, AR4.D, AR4.E, AR4.G, AR4.H, and AR5) in 2012 and 2013. Samples were collected from scour pools along the stream margin for 48 hours twice yearly in August. Previous work has indicated that pools have higher rates of emergence (Iwata 2007, Malison et al. 2010). Floating emergence traps were modified from Malison et al (2010). Traps had the same base dimensions (0.33 m²), but the

shape was changed to a pyramid, and a collection bottle filled with 80% ethanol was added. The pyramid shape was employed in order to funnel insects toward the bottle, and the bottle was added in order for a single technician to collect numerous ($n > 20$) samples per day. Emergence samples were sorted and identified in the lab. All Ephemeroptera, Plecoptera, and Trichoptera taxa were identified to genus, and all other orders were identified to family. After identification, samples were grouped into orders and were then dried at 60°C for 48 hours in order to obtain dry mass (Saunders and Fausch 2012).

Adult aquatic and terrestrial invertebrate inputs were assessed at the same six sites where emergence was collected using plastic pan traps (100 cm X 41 cm X 15 cm deep) placed along the stream bank. Three pan traps were deployed for 48-hour intervals twice per year in August 2012 and 2013. Samples were collected in August, when terrestrial inputs were hypothesized to be greatest (Saunders and Fausch 2012). Pans were filled with stream water and approximately 5 mL of unscented, biodegradable surfactant to reduce surface tension. Pans were selectively placed at each site to sample three habitat types: willow, grass, and gravel bars. I selected locations that had homogenous habitat for at least 5 m upstream, downstream, and lateral of the pan placement in order to minimize variation. Because some sites did not have all three habitat types adequately represented, I placed two pan traps in one habitat category (i.e. site AR4.E did not have the willow habitat represented, so I placed two pan traps in grass habitats, and one in the gravel category). I selected these three habitat types for three reasons; 1) these three categories are the dominant habitat types present along this reach; 2) preliminary analysis from pan traps placed randomly in 2010 and 2011 indicated large differences in total number of invertebrates based on bank vegetation (Pomeranz, unpublished data); 3) the proposed in-stream and bankside habitat modifications will include gravel bars and other structures to induce meanders and willow plantings in order to reinforce eroding banks. I wanted to assess how these three habitats affect total invertebrate inputs and how future habitat modifications may affect this input.

Invertebrates were removed from the pan traps using a small aquarium net and preserved in 80% ethanol. Adult aquatic insects were identified to the lowest practical taxonomic unit, usually genus or family, and terrestrial invertebrates were identified to the lowest practical level. Most adults were identified to family, while most larvae were identified to order. I considered all taxa that utilize aquatic habitats for part of their life history as aquatically derived, and all taxa that only utilize terrestrial habitats for all of their life history as terrestrial (Saunders and Fausch 2007).

To obtain estimates of biomass, invertebrates were enumerated and sorted into the following categories and dried at 60°C for 48 hours (Saunders and Fausch 2012): Ephemeroptera, Plecoptera, Trichoptera, Chironomidae, Aquatic Diptera, Terrestrial Diptera, Terrestrial Other and Aquatic Other (coleopterans, hemipterans, molluscs, oligochaetes, and hydrachnids). I separated the Dipteran family Chironomidae because this was the numerically dominant group, and I separated terrestrial Diptera from the other terrestrial groups because this was the only terrestrial group that was sufficiently abundant to get a reliable dry weight. Occasionally, the invertebrates collected within a taxonomic group occurred in such low abundances that their dry weights were within the measurement error of the balance. In these cases the observation was deleted from the database.

Brown Trout Diets

Brown trout (*Salmo trutta*) stomach contents were collected at four sites (AR4.C, AR4.E, AR4.G, and AR4.H) using bank electroshocking on 15-16 August, 2012, and using a backpack electroshocker on 15 August 2013. Stomach samples were collected in August because this is when terrestrial inputs are expected to be the highest in Rocky Mountain streams (Saunders and Fausch 2007). I collected fish stomach samples (n=17-25 per site) for 2 years in order to quantify the natural annual variability in feeding habits. Fish were anesthetized in the field using CO₂, and stomach contents were removed using gastric lavage (Waters et al. 2004, Saunders and Fausch

2007). Only fish between 120-300 mm fork length were selected because larger fish become piscivorous and are difficult to sample effectively (Saunders and Fausch 2007). Fish weights (+/- 1g) were also recorded in the field. Because total length (TL) was measured in 2012 and fork length (FL) was measured in 2013 I used the following equation to convert TL to FL (FishXing 2006):

$$TL = FL * 1.037 \text{ (formula 1)}$$

Stomach contents were sieved through a 250 µm screen and preserved in ethanol in the field. Fish were allowed to recover in a live well before being returned to the study reach. In the laboratory, aquatic larvae and adults were identified to the lowest taxonomic unit, usually genus, and terrestrial insects were identified to family. Insects were then pooled into the following categories and dried for 48 hrs at 60°C: Ephemeroptera, Plecoptera, Trichoptera, Aquatic Diptera, Aquatic Other (coleopterans, hemipterans, molluscs, oligochaetes, and hydrachnids), and Terrestrial. These categories were selected in order to determine the relative weight contributions to brown trout feeding habits and to compare prey utilization with prey availability.

Statistical Analyses

All statistical analyses were conducted using the program R (R Core Team 2013). Repeated-measures analysis of variance (ANOVA) was used to test for differences in total invertebrate abundances and dry weights, and the abundance and dry weights of both aquatic and terrestrial invertebrates.

This study was designed to examine the effects of bankside vegetation on invertebrate input into the stream, and to assess the annual variation of this input. For these reasons, I used linear models and tested the main effects of Year and Habitat, as well as the Year*Habitat interaction.

All dry weights and abundance data were log transformed in order to satisfy assumptions of parametric statistics. Abundance and biomass data was all converted to units per m² per day for

direct comparison. Analysis of covariance (ANCOVA) was used to determine if fish size influenced the amount of terrestrial prey items consumed. Finally, I analyzed the total proportion of aquatic and terrestrial prey items in order to determine the dominant prey resource, by weight, in this system. I used the non-parametric Wilcoxon Signed Rank test because numerous fish consumed no terrestrial items, thus causing the distribution to be highly skewed

All models were ranked using Akaike Information Criterion corrected for small sample size (AIC_c). Models with $\Delta AIC_c < -2$ from the top model were considered to have equal support, and models with $\Delta AIC_c > -2$ were considered to be not supported by the data (Anderson and Burnham 2002).

Results

Invertebrates

Benthic macroinvertebrate samples from all sites were similar within years ($P=0.5948$), so data were pooled. The total number of benthic macroinvertebrates collected in summer 2013 was approximately 1.6 times the number sampled in 2012 ($P= <0.001$, Figure 1.1). Relative abundance of orders was similar between years, except for the marked decrease in Ephemeroptera in 2013 (21.4 to 6.5%), and an increase in the relative proportion of aquatic Diptera in 2013 (50.0 to 73.0%) (Figure 1.2).

There was no spatial heterogeneity in aquatic insect emergence, so again all sites were pooled for analysis. An estimated 258 and 162 aquatic insects emerged per m^2 in 2012 and 2013, respectively (Figure 1.3). There was a significant decrease in the total number of emerged aquatic insects in 2013 compared with 2012 ($p=0.007$). Aquatic insect emergence in August of 2012 and 2013 was dominated by Diptera (89 to 69% respectively), and Trichoptera (10 and 24% respectively). The relative contribution of Ephemeroptera in 2012 and 2013 was 1 and 6% respectively. Plecoptera and other aquatic insects each contributed $<1\%$ in both years.

There was no significant differences in emerging biomass between sites, but there was again a significant difference between years ($P=0.008$). I estimated that 85.5 and 134.62 mg of adult aquatic insects emerged per m^2 in 2012 and 2013, respectively. Unlike the abundance data, the biomass of emergent aquatic insects increased approximately 1.6 times in 2013 compared with 2012. Dry weights in both years were dominated by aquatic Diptera (51 and 29%, respectively), and Trichoptera (31 and 40%, respectively). Despite comprising $<1\%$ of the abundance in both years, Plecopterans contributed 4 and 10% of the total biomass collected in 2012 and 2013 respectively. Likewise, Ephemeroptera contributed 9 and 12% of the total emergent biomass collected.

An average of 1173.1 insects per $m^{-2} d^{-1}$ were collected in pan traps over the two year period. When averaged over both years, there was no difference in total invertebrate abundance among habitat categories. However, I observed significant annual variation in total abundance. Although Grass and Willow had similar total invertebrate abundances in both years, Gravel had nearly twice as many total invertebrates in 2013 as in 2012 (Figure 1.4). The top 2 models based on AIC_c rankings had equal support ($\Delta AIC_c < 2$) (Table 1.2). The top model included only the main effect of Year, and this was found to be a significant predictor of total invertebrate abundance ($P=0.0080$). The second model contained both main effects of Year and Habitat as well as the Year*Habitat interaction term, but none of these factors were significant. It is also important to note that these two top models only explained 9.0 and 14.0% of the variation, respectively (adjusted R^2 values).

Adult aquatic insect input abundances followed patterns very similar to total invertebrate abundances, primarily because aquatic adults comprised the vast majority of the organisms collected in all pan traps (Figure 1.3b). When averaged over both years, all habitat categories had similar abundances of adult aquatic insect inputs. When averaged over the three habitat categories,

a significantly higher number of adult aquatic insects were collected in 2013 than in 2012 (Year $P=0.0096$). Indeed, the top model for adult aquatic insect inputs included only the main effect of Year. The abundances of adult aquatic insect inputs in the Grass and Willow category were similar for both years, while the abundance in the Gravel category was nearly twice as high in 2013 as in 2012 (Figure 1.3b). Again, the top model for adult aquatic insect abundances only accounted for 8.5% of the variation (adjusted R^2 value).

When averaged over both years, there was a highly significant effect of habitat type on the abundance of terrestrial invertebrates ($P<0.0001$). The Grass and Willow categories received 5.9 and 4.4 times as many terrestrial invertebrates as the Gravel category, respectively. The Grass category received 1.3 times as many terrestrial invertebrates as the Willow category, although this was not significant (one sided T-test $P=0.0847$). When averaged over all three habitat categories, there was a slightly significant effect of Year on total abundance of terrestrial invertebrates ($P=0.0152$). Similar to both the total and adult aquatic insect abundances, there was a higher number of terrestrial invertebrates in the Gravel category in 2013 than in 2012, although the Year * Habitat term was not selected based on AIC_c rankings. Interestingly, in contrast to the models for total and adult aquatic insect abundances, the top model for terrestrial invertebrate abundances accounted for 70.0% of the variation (adjusted R^2 value).

On average, sites received 75.3 mg m^{-2} per day of total invertebrate biomass. Averaged across all sites, total invertebrate biomass was approximately 2 times greater in 2013 as in 2012 ($P<0.0001$, Figure 1.5). Additionally, habitat had a highly significant effect on the biomass of total invertebrate input averaged over both years ($P<0.0001$). Pan traps placed in willow and grass habitats received between 3.2 and 4.4 times as much total invertebrate dry weights as pan traps placed in gravel habitats, respectively. Pan traps placed in grass habitats received 1.4 times as much

total invertebrate dry weights as pan traps placed in willow habitats, although this finding was not statistically significant due to high variation (two sided two sample T-test; $P=0.19$).

Adult aquatic invertebrate biomass followed a similar pattern as total invertebrate biomass. On average the Arkansas River received 47.3 mg m^{-2} per day of adult aquatic insects. Adult aquatic invertebrate inputs were 2.4 times as high in 2013 than in 2012 ($P<0.0001$, figure 1.5b). Again, averaged over all sites, pan traps placed in each of the three habitat categories showed an increase in aquatic invertebrate dry weights in 2013. Pan traps placed in all three habitats had a >2 times increase in aquatic insect biomass in 2013.

Habitat category also had a highly significant effect on the dry weight of aquatic invertebrates ($P<0.0001$). Pan traps placed in willow and grass habitats received between 2.9 and 4.1 times as much aquatic invertebrate dry weights as pan traps placed in gravel habitats, respectively. Pan traps placed in grass habitats received 1.4 times as much aquatic invertebrate dry weights as pan traps placed in willow habitats, although this finding was not significant due to high variation (two sided two sample T-test; $P=0.25$).

Terrestrial invertebrate input into the Arkansas River was much lower than adult aquatic insect input. On average, the river received 28.0 mg m^{-2} per day of terrestrial invertebrates. Unlike adult aquatic insect inputs, terrestrial invertebrate inputs were similar between years, and comprised 26.6 and 14.4% of the total invertebrate dry weights in 2012 and 2013, respectively. Gravel habitats received an average of 6.7 mg m^{-2} per day, while grass and willow habitats received an average of 42.6 and 39.2 mg m^{-2} per day respectively.

The two top models of terrestrial invertebrate dry weight input had equal support based on AIC_c rankings: Habitat and Year + Habitat. In both models, Habitat was highly significant ($P<0.0001$). When Year was included in the model, it was not a significant predictor of terrestrial invertebrate dry weights ($P=0.1824$). Indeed, the dry mass of terrestrial invertebrates was similar

in all three categories in both years (Figure 1.5c). Both of these models accounted for 73.12 and 73.19% of the variation (Table 1.3).

Pan traps placed in gravel and grass habitats showed an increase in terrestrial invertebrate dry weights of 1.3 and 1.2 times in 2013 compared to 2012. In contrast, pan traps placed in willow habitats showed a slight decrease in terrestrial invertebrate inputs (0.98 times as much in 2013 than in 2012). Pan traps placed in the grass and willow habitat received an average of 6.8 and 5.9 times as much terrestrial invertebrate biomass than pan traps placed in the gravel category.

Trichopterans were proportionately the dominant group by weight in all habitat categories and in both years, except for in the grass category in 2013 (Figure 1.6). Aquatic Diptera (including Chironomidae) were the dominant group by weight in the grass category in 2013, and the second most dominant group in all other year-category combinations.

Fish diets

Across all sites, dry weights of brown trout stomach contents were approximately 2 times greater in 2013 than in 2012 ($P = <0.0001$, Figure 1.7). Fish from all sites had increased prey biomass in 2013, except for fish from AR4.H, which had similar total weights in both years. Dry weights of stomach contents weights from site AR4.H in 2012 were between 2.2 and 2.6 times heavier than stomach samples from the other three sites (Site*Year interaction; $P=0.0005$). Site was not a significant main effect due to high variability in total dry weights ($P=0.6425$). Total dry weight of prey contents in fish that consumed terrestrial invertebrates was approximately 2 times greater than in fish that avoided terrestrial prey, but this effect was not significant due to high variation ($p=0.5046$). However, fish from site AR4.H that consumed terrestrial invertebrates had significantly greater prey biomass than fish that only consumed aquatic insects (Site * "Has Terrestrial" interaction; $P=0.0169$). Within years, all fish consumed approximately the same amount of aquatic

prey, regardless of consuming terrestrial prey or not. Additionally, I did not find that larger fish consumed more total prey resources than smaller fish ($P=0.43$).

Terrestrial invertebrates comprised only 4.5 and 10.0% of total invertebrate biomass from brown trout stomach samples in 2012 and 2013, respectively. Although there were no significant differences among sites, fish generally consumed higher amounts of terrestrial invertebrate prey in 2013. Site AR4.H had the highest percentage of terrestrial biomass in both years (7.5 and 18.7% respectively). A significantly higher proportion of fish contained terrestrial invertebrates in their stomachs in 2013 (54%) than in 2012 (30%) ($P = 0.0039$) and terrestrial invertebrate biomass was 2.7 times greater in 2013 than in 2012 ($P=0.0014$, Figure 1.8b). Also, larger fish did consume slightly more terrestrial biomass than smaller fish (ANCOVA, $P=0.0310$). This pattern was generally consistent across all sites.

Aquatic insect dry weights followed patterns similar to the total stomach dry weights (figure 1.7c). Aquatic insects made up a majority of the total dry weights in both 2012 and 2013 (95.5 and 90% respectively). In 2012 and 2013, 83% and 80% of the dry weights in trout stomachs was constituted of benthic aquatic insects. Although the relative proportions of aquatic insect dry weights were similar between years, the total dry weight of aquatic insects averaged over all sites was 1.9 times greater in 2013 than in 2012 ($P<0.0001$). All sites showed an increase in aquatic insect dry weights in trout diets in 2013 except for site AR4.H.

Fish that consumed terrestrial insects also consumed 1.5 to 1.2 times the dry weights of aquatic invertebrates, in 2012 and 2013 although this was not significant ($p=0.29$). In fish that did consume terrestrial invertebrates in 2012 and 2013, terrestrial invertebrates comprised 29-39% of their total stomach contents. Likewise, in fish that did consume terrestrial subsidies, I did find that larger fish consumed slightly more terrestrial dry weights than smaller fish ($P=0.0310$)

The relative composition in trout diets of mayflies, stoneflies, caddisflies, aquatic dipterans, other aquatic taxa (coleopterans, hemipterans, molluscs, oligochaetes, and hydrachnids), and terrestrial invertebrates varied among sites and between years (Figure 1.8). Although dry weights increased in 2013 for all categories, the relative contributions showed no consistent patterns. The proportion composition of mayflies, stoneflies, aquatic Diptera, and other aquatic taxa decreased in 2013, whereas the relative contributions of caddisflies and terrestrial invertebrates increased. Despite these changes in relative abundance, caddisflies were consistently the most important group in 2012 and 2013, comprising 48.8 and 57.1% of total prey biomass, respectively. The second most important group, based on dry weights, in 2012 and 2013 were the aquatic Diptera (27.5 and 15.1% respectively).

Brown trout exhibited a high degree of variation in their individual diets. For example, the average occurrence of *Glossosoma* spp. (Trichoptera: Glossosomatidae) larvae in fish diets was 3 per fish, but ranged between 0 and 68, while the average occurrence of *Baetis* spp. (Ephemeroptera: Baetidae) larvae was 5 per fish and ranged between 0 and 95. Likewise, the Gastropod family Physidae had an average occurrence of 0.57 per fish, but ranged from 0 to 68, and the average occurrence of Chironomidae (Diptera) adults was only 1.9 per fish, but ranged from 0 to 81.

Discussion

Abundance of adult aquatic insect inputs into the Arkansas River did not have a strong relationship with riparian habitat. Inputs were similar among habitats and between years, except in the gravel, where adult aquatic insect abundances were approximately doubled. Adult aquatic insects are generally found close to stream margins (Jackson and Resh 1989) regardless of the riparian vegetation present (Bridcut 2000). Iwata et al (2003) found that the number of aquatic adults decayed exponentially with increasing distance from stream margins. Many aquatic insects have life histories with short adult phases, some only lasting for a few hours. During this short time, individuals must emerge, successfully mate, and females must return to the water surface to lay

their eggs. The probability of successfully completing these steps likely increases with limited travel time and distances. The relatively consistent inputs of adult aquatic insects is likely due to the fact that pan traps are placed along stream margins, and this is where the adults spend a majority of their short lives. This may also explain why the top model for aquatic insect inputs only explained 8.5% of the variation, compared with 73.1 and 73.2% of the variation explained in the model for terrestrial input.

Although adult aquatic insect abundances showed similar values in most habitat categories in both years, the dry weights of adult aquatic insects were nearly twice as large in 2013 compared to 2012. This is likely due to the slightly different community composition present in both years. For example, the Trichoptera inputs in 2012 were dominated by the family Hydroptilidae, a relatively small caddisfly. In 2013, however, there were fewer hydroptilids, and an increased abundance of larger Brachycentridae and Glossosomatidae caddisflies. Another example is that members of the Tipulidae family, a medium to large bodied Diptera, were over twice as abundant in 2013. This may partially explain why the abundance of aquatic insects was similar in both years, but the biomass input was so much greater in 2013. Abundance data can often be misleading, particularly in food web studies. Biomass estimates are important in these studies as this is the endpoint that matter matters for fish production.

Some of the annual variation in invertebrate input and feeding habits of brown trout may be related to differences in flow regimes between years. In 2012, the mean annual discharge was 113 cfs (cubic feet per second), while 2013 was 226 cfs (USGS gauge 07083710). Likewise, in 2011, the year prior to this current study, the mean annual discharge was 801 cfs. There are two likely hypotheses to explain the marked difference in adult aquatic insect inputs between the two years: 1) increased flow in 2013 was beneficial for aquatic insect larvae and allowed more individuals to survive to adulthood; 2) larval densities were reduced by extremely high flows in 2011, and

required at least two years to recover. Although it is not possible to discern the mechanism, larval densities in 2013 were approximately double that in 2012, lending support to the former hypothesis.

Terrestrial invertebrate abundances and dry weights showed little annual variation, with relatively similar inputs within categories between years. Although there was little annual variation, terrestrial inputs showed a strong relationship with habitat type. The vegetated categories (willow and grass) both had higher abundance and biomass inputs than the un-vegetated gravel category. Since these inputs were consistent among the habitats between years, it lends support to the idea that terrestrial invertebrates are dependent on riparian vegetation (Southwood 1961, Mason and MacDonald 1982, Wipfli 1997, Kawaguchi and Nakano 2001, Allan et al. 2003, Saunders and Fausch 2007). In addition, this may explain why the models of terrestrial inputs explained a greater amount of the variation than the model for aquatic insect inputs.

I hypothesized that the willow category would have the highest abundance of terrestrial invertebrates due to the more complicated 3-D architecture of willow trees, and the increased surface area available. In contrast, I found higher terrestrial invertebrate abundances in the grass habitat, although this finding was not significant. Likewise, I hypothesized that the grass habitat would have higher total terrestrial invertebrate biomasses due to the presence of large taxa such as Orthopterans (Edwards and Huryn 1995, Jonas and Joern 2008). I hypothesized that the presence of Orthopterans would be an important component to fish diets because of their generally large size; a single grasshopper can provide the nutritional content of numerous smaller insects. Although I did find one Orthopteran in the grass habitat in 2011 during the pilot phase of this study, I did not collect a single one in 2012-13. Although terrestrial invertebrate biomass was higher in grass than the willows, this again was not statistically significant.

Average input of terrestrial biomass is similar to what has been found in other Western streams (Saunders and Fausch 2012), but was highly variable based on riparian vegetation (6.7-42.6 mg m⁻² d⁻¹). This lends support to my hypothesis that riparian vegetation plays a critical role in maintaining terrestrial-aquatic linkages. Although my hypotheses regarding the differences between vegetation categories were not supported, the average input of terrestrial biomass in the vegetated categories (willow and grass), was significantly greater than the gravel habitat.

Terrestrial invertebrates only constituted 4.5 and 10% by weight, of total brown trout diets in 2012 and 2013 respectively. This value is much lower than results presented in other studies of salmonidae diets conducted in western streams, despite finding similar inputs of terrestrial biomass (Baxter et al. 2005, Saunders and Fausch 2007, 2012). Most of the previous studies examining the importance of terrestrial prey items in salmonidae diets have been conducted in small, 1st to 3rd order streams with a low width to edge ratio. Although the inputs were similar in this larger stream, it is likely that the density of terrestrial invertebrates per m² of flowing water was much lower.

In addition to previous studies being conducted on smaller streams, they also generally examined other members of the salmonidae family, such as rainbow, cutthroat and brook trout. Indeed, Saunders and Fausch (2012) found that the reliance on terrestrial prey items was weaker in brown trout than in other salmonids sampled (Saunders and Fausch 2012, figure 6a). It may be that the combination of fish species and a high stream width to edge ratio interacted to reduce the importance of terrestrial prey for brown trout in the Arkansas River.

Additionally, I found no relationship between brown trout size and total stomach dry weights, and only a weak relationship between trout size and terrestrial dry mass in diets (P=0.0310). This may be due to feeding rates in brown trout decreasing with size (Bachman 1984), or due to the low density of drifting terrestrial prey. Many fish assume dominance hierarchies

based on fish size (Gowan and Fausch 2002, Saunders and Fausch 2012), with the largest fish occupying the best habitat. Saunders and Fausch (2012) showed that larger rainbow, cutthroat and brook trout consumed more terrestrial invertebrates in low order Rocky Mountain streams. However, this relationship was less pronounced for brown trout (Saunders and Fausch 2012, Figure 6a). Indeed, large brown trout (relative size, see methods in Saunders and Fausch 2012) in their study consumed far less terrestrial invertebrates than the other species.

Brown trout have been shown to have significant variation in their diets, both among and within populations, and even within individuals throughout space and time, largely based on prey availability (Bridcut and Giller 1995). All fish consumed approximately equivalent amounts of aquatic prey. However, the average dry weight of stomach contents in individual fish that did consume terrestrial insects was approximately two times greater. Although this difference was not significant, it supports the idea that some individual fish may have specialized on terrestrial invertebrate prey or held specific foraging locations that allowed them to use most of the terrestrial invertebrate inputs. The variation of fish diet could be explained through individuals identifying a specific search pattern and therefore consuming more of that prey resource relative to other fish, or through spatial location within the stream; certain locations have higher availability or more favorable foraging conditions for certain prey items, and fish distribute themselves in order to maximize energy intake (Gowan and Fausch 2002).

One interesting finding, however, was the significant increase in proportion of fish that consumed terrestrial prey in 2013, as well as the significant overall increase in terrestrial invertebrate consumption in 2013, despite the relatively consistent input between the two years. This may be due to the increase in adult aquatic invertebrate biomass inputs, as well as increased numbers of benthic invertebrates in 2013. Since brown trout in this system are predominantly consuming aquatic invertebrates, an increase in their availability may have caused an increased

foraging response in trout. This may have caused an incidental increase in terrestrial invertebrate consumption. This is contrary to what many other studies have found. The reciprocal subsidies paradigm (Baxter et al. 2005) puts forth that salmonids increase their consumption of terrestrial invertebrates when availability of aquatic invertebrates is low (Wipfli 1997, Kawaguchi and Nakano 2001, Utz and Hartman 2007). In the present study, it appears that brown trout are increasing their consumption of terrestrial invertebrates as an indirect response to increased availability of aquatic prey resources. To my knowledge, this is a novel response not previously documented.

It is also interesting to note that fish, on average, consumed similar amounts of aquatic insect dry mass within years, regardless of consumption of terrestrial invertebrates. This caused fish that did consume terrestrial invertebrates to have total stomach contents that weighed approximately twice as much as fish that did not consume terrestrial invertebrates. Although terrestrial invertebrate subsidies were not equally distributed throughout all fish sampled in this study, they were still an important component of trout diets in the fish that were able to utilize this subsidy. This also supports the idea that individual fish were able to identify a specific search image for specific prey resources (Ringler 1979), or that they were foraging in locations that allowed them to more easily utilize the terrestrial subsidy.

Many river restoration projects have the stated goal of maintaining or improving a productive fishery for ecological and economic reasons (Bernhardt et al. 2005). This study highlights the importance of maintaining terrestrial-aquatic linkages in order to provide critical subsidies to fish populations. Terrestrial input rates are much higher along vegetated banks (this study, Saunders and Fausch 2007, 2012). In areas lacking riparian vegetation, the terrestrial input to the stream is dramatically reduced, and may even be severed. Although brown trout were not consuming large amounts of terrestrial invertebrates and were not as reliant on terrestrial subsidies as has been shown in other studies, average prey dry weight of individual fish that

consumed terrestrial invertebrates were approximately 50% greater than fish that did not consume terrestrial invertebrates. I have demonstrated that if the quantity of riparian vegetation was improved along the Arkansas River, it would increase the terrestrial subsidy available to brown trout. If the input of terrestrial invertebrates increased, this could increase the drift density of terrestrial invertebrates, and may be utilized by more fish in the population.

This study also provides evidence that it is more beneficial to rehabilitate riparian corridors with vegetation of any type, as opposed to the commonly used rip-rap. The gravel bars can be viewed as a surrogate for large boulder and concrete rip-rap bank stabilization treatments. I have shown that these large, un-vegetated areas provide reduced adult aquatic insect inputs and very low, terrestrial invertebrate inputs. Based on these findings, I recommend riparian vegetation to be a useful restoration and management goal for river systems. Many restoration activities focus on in-stream parameters such as pool depth and flow velocity, and engineer the river with these factors in mind. It has been shown, however, that these restoration measures do not always cause fish or benthic invertebrate communities to recover (Bernhardt and Palmer, 2011). In contrast, this study has shown that improved riparian vegetation does have a direct increase in terrestrial subsidy inputs, and these benefits can be utilized directly by salmonids. This information can be used to inform future management and restoration activities in impacted watersheds. Further study is currently being conducted to see how the restoration activities in the Upper Arkansas River will affect these terrestrial-aquatic linkages, and how they impact the brown trout population in these reaches.

Implications

Terrestrial inputs to stream ecosystems are strongly related to riparian vegetation (Mason and MacDonald 1982, Allan et al. 2003). I have shown that vegetated banks provide significantly more terrestrial subsidies to streams than non-vegetated banks. It is important to maintain

terrestrial-aquatic linkages in streams and their associated riparian zones by promoting and maintaining diverse and healthy riparian vegetation. This may be as simple as excluding grazing rights from riparian zones, or re-planting riparian vegetation, and utilizing “green” bank stabilization techniques. Willow plantings, when given enough time to successfully establish, have been shown to withstand erosive forces similar to traditional rip-rap (Schiechtel 1994). These willow plantings can prevent further bank erosion, provide shade, as well as promote terrestrial invertebrate input to streams. In habitats such as the Upper Arkansas River, which currently receive minimal terrestrial invertebrate subsidies, increasing riparian vegetation throughout the restoration reach may increase the total invertebrate inputs and directly improve the resident brown trout population.

Tables and Figures

Table 1.1 Geographic information for study sites and USGS Gauge located within the restoration reach on the Upper Arkansas River. Drainage area is in km².

Geographic information for the restoration reach along the Upper Arkansas River Basin

Site	Latitude	Longitude
AR4.C	39 09' 52.9"	106 19' 11.9"
AR4.D	39 09' 45.3"	106 19' 07.6"
AR4.E	39 09' 33.2"	106 19' 07.5"
AR4.G	39 08' 22.7"	106 18' 57.5"
AR4.H	39 08' 03.4"	106 18' 56.2"
AR5	39 07' 39.0"	106 18' 38.8"

USGS Gauge, Arkansas River Below Empire Gulch, near Malta, Colorado

Drainage Area	Latitude	Longitude
616	39°09'50"	106°19'10"

Table 1.2 Top four models based on AIC_c rankings for total invertebrate, aquatic invertebrate, and terrestrial invertebrate abundance inputs to the Upper Arkansas River Basin in 2012 and 2013.

Total Invertebrate Abundance	Main Effects	Interactions	p	AIC _c	Delta	exp	sum exp	wi	Adjusted R ²
Year	1	0	1	108.977	0.00	1.00	1.69	0.59	0.0897
Year+Habitat+Year*Habitat	2	1	3	110.474	-1.50	0.47		0.28	0.1394
Year+Habitat	2	0	2	112.135	-3.16	0.21		0.12	0.0808
Habitat	1	0	1	117.543	-8.57	0.01		0.01	-0.0157
Aquatic insect Abundance	Main Effects	Interactions	p	AIC _c	Delta	exp	sum exp	wi	Adjusted R ²
Year	1	0	1	120.477	0.00	1.00	1.33	0.75	0.0849
Year+Habitat+Year*Habitat	2	1	3	124.038	-3.56	0.17		0.13	0.1079
Year+Habitat	2	0	2	124.226	-3.75	0.15		0.11	0.0678
Habitat	1	0	1	129.176	-8.70	0.01		0.01	-0.0231
Terrestrial Insect Abundance	Main Effects	Interactions	p	AIC _c	Delta	exp	sum exp	wi	Adjusted R ²
Year+Habitat	2	0	2	108.787	0.00	1.00	1.48	0.67	0.6976
Year+Habitat+Year*Habitat	2	1	3	110.905	-2.12	0.35		0.23	0.7005
Habitat	1	0	1	112.766	-3.98	0.14		0.09	0.6729
Year	1	0	1	185.432	-76.64	0.00		0.00	0.0146

Table 1.3 Top four models based on AIC_c rankings for total invertebrate, aquatic invertebrate, and terrestrial invertebrate dry weights inputs to the Upper Arkansas River Basin in 2012 and 2013.

Total Invertebrates Dry Weights	Main Effects	Interactions	p	AIC _c	delta	exp	sum exp	wi	Adjusted R2
Year+Habitat	2	0	2	22.23	0.00	1.00	1.04	0.96	0.8682
Year*Habitat	2	1	3	28.54	-6.31	0.04		0.04	0.8958
Habitat	1	0	1	45.73	-23.50	0.00		0.00	0.7103
Year	1	0	1	79.61	-57.38	0.00		0.00	0.1237
Aquatic Invertebrates Dry Weights	Main Effects	Interactions	p	AIC _c	delta	exp	sum exp	wi	Adjusted R2
Year+Habitat	2	0	2	48.63	0.00	1.00	1.06	0.95	0.7302
Year*Habitat	2	1	3	54.40	-5.77	0.06		0.05	0.7147
Habitat	1	0	1	71.12	-22.50	0.00		0.00	0.4252
Year	1	0	1	77.21	-28.58	0.00		0.00	0.2705
Terrestrial Invertebrates Dry Weights	Main Effects	Interactions	p	AIC _c	delta	exp	sum exp	wi	Adjusted R2
Habitat	1	0	1	53.85	0.00	1.00	1.72	0.58	0.7312
Year+Habitat	2	0	2	54.61	-0.76	0.68		0.40	0.7319
Year*Habitat	2	1	3	60.40	-6.54	0.04		0.02	0.7240
Year	1	0	1	94.90	-41.05	0.00		0.00	-0.0171

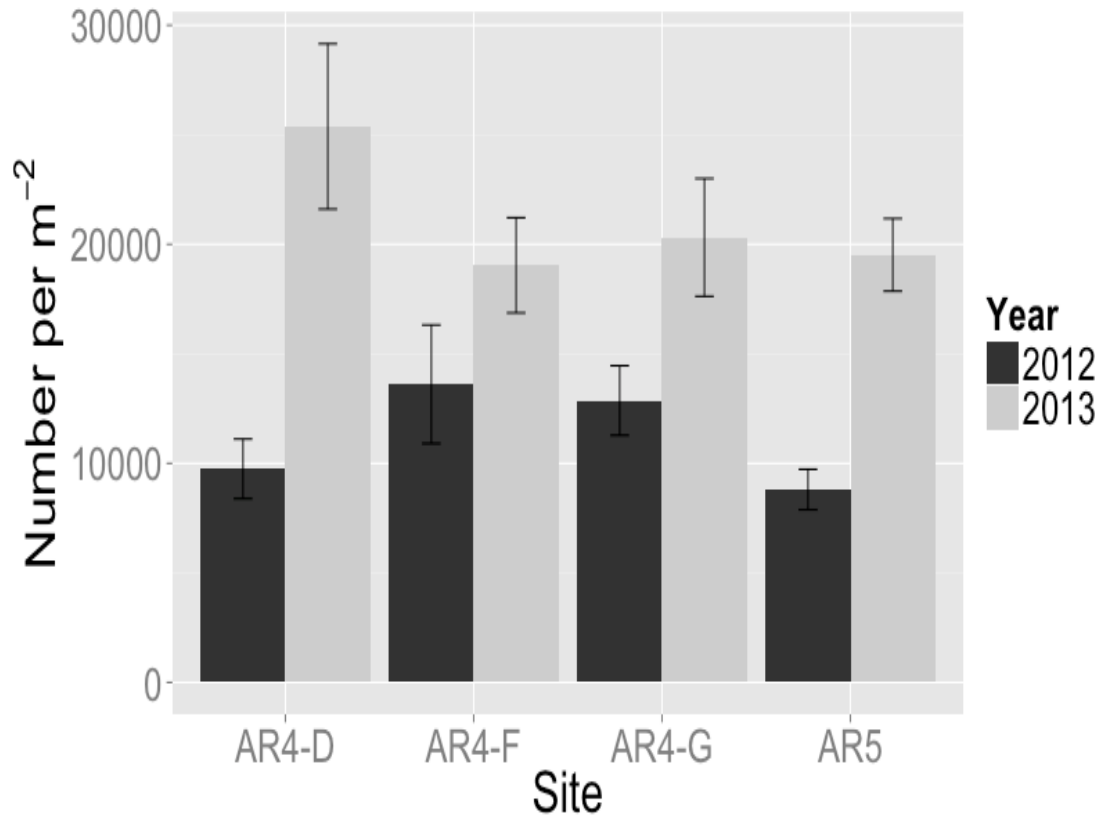


Figure 1.1 Mean (\pm SE) benthic densities from four sites in the Upper Arkansas River in 2012 and 2013.

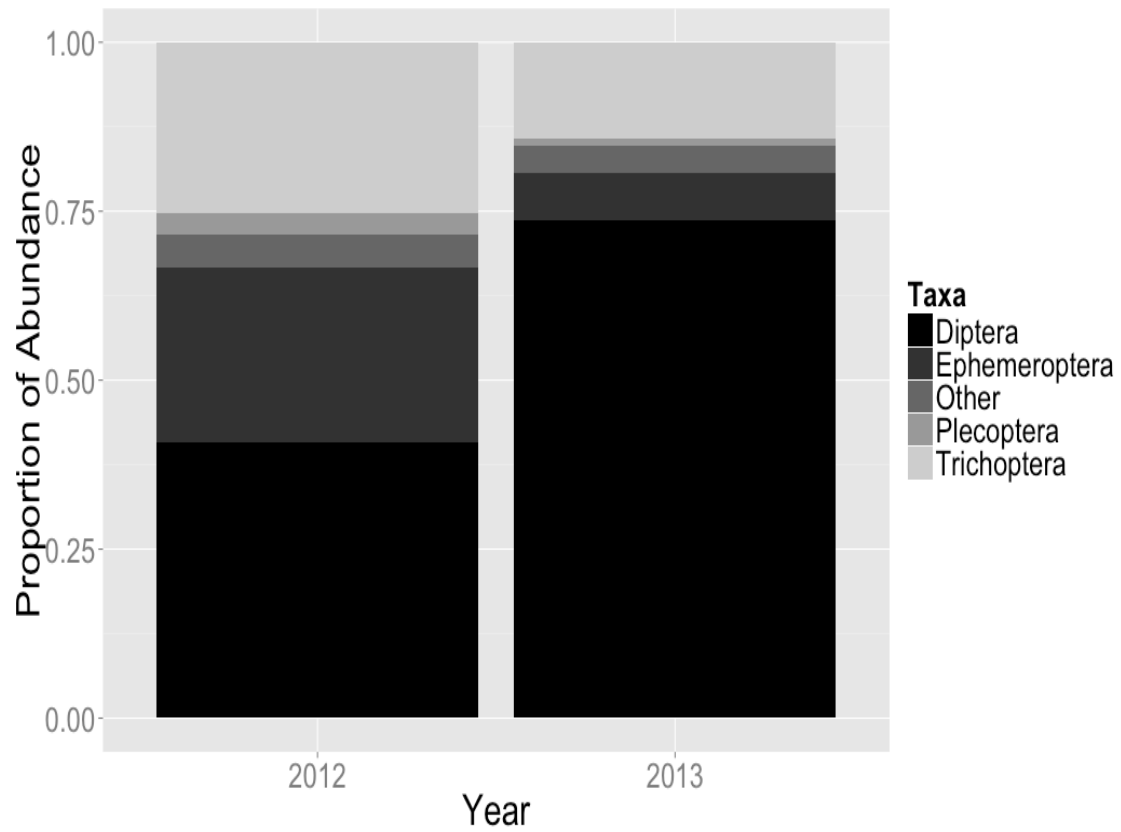


Figure 1.2 Relative contributions of orders to total benthic densities in the Upper Arkansas River Basin in 2012 and 2013.

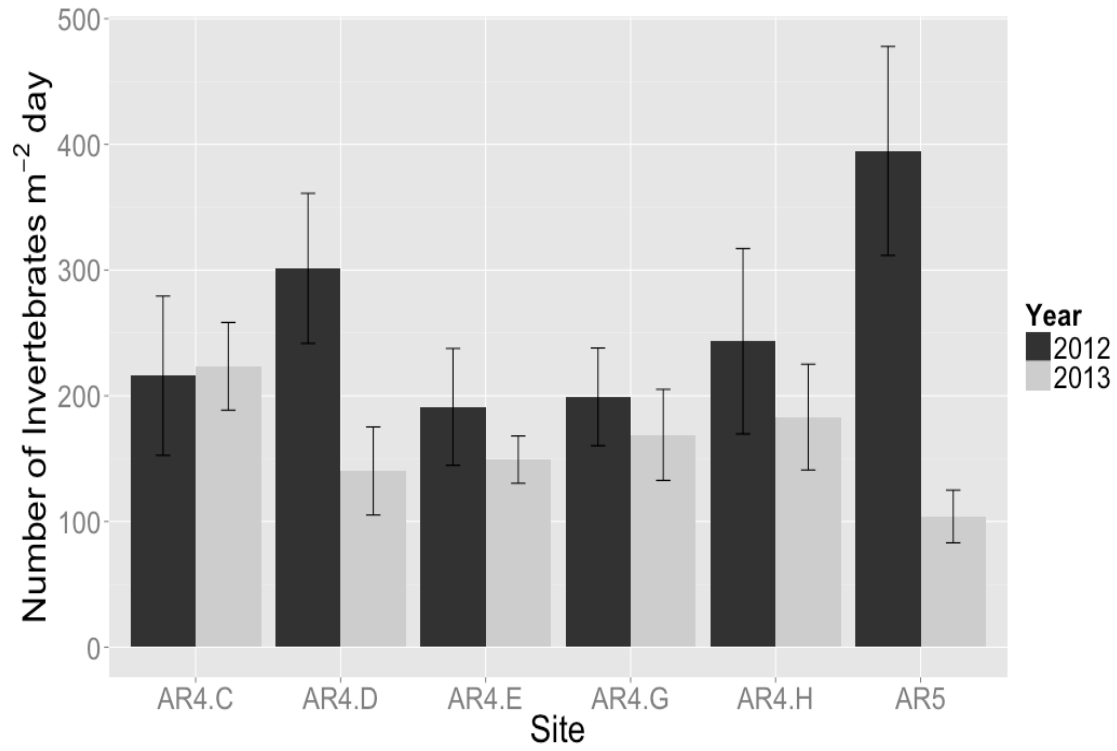


Figure 1.3 Mean (\pm SE) number of emerging aquatic insects per m² from six sites in the Upper Arkansas River basin in 2012 and 2013

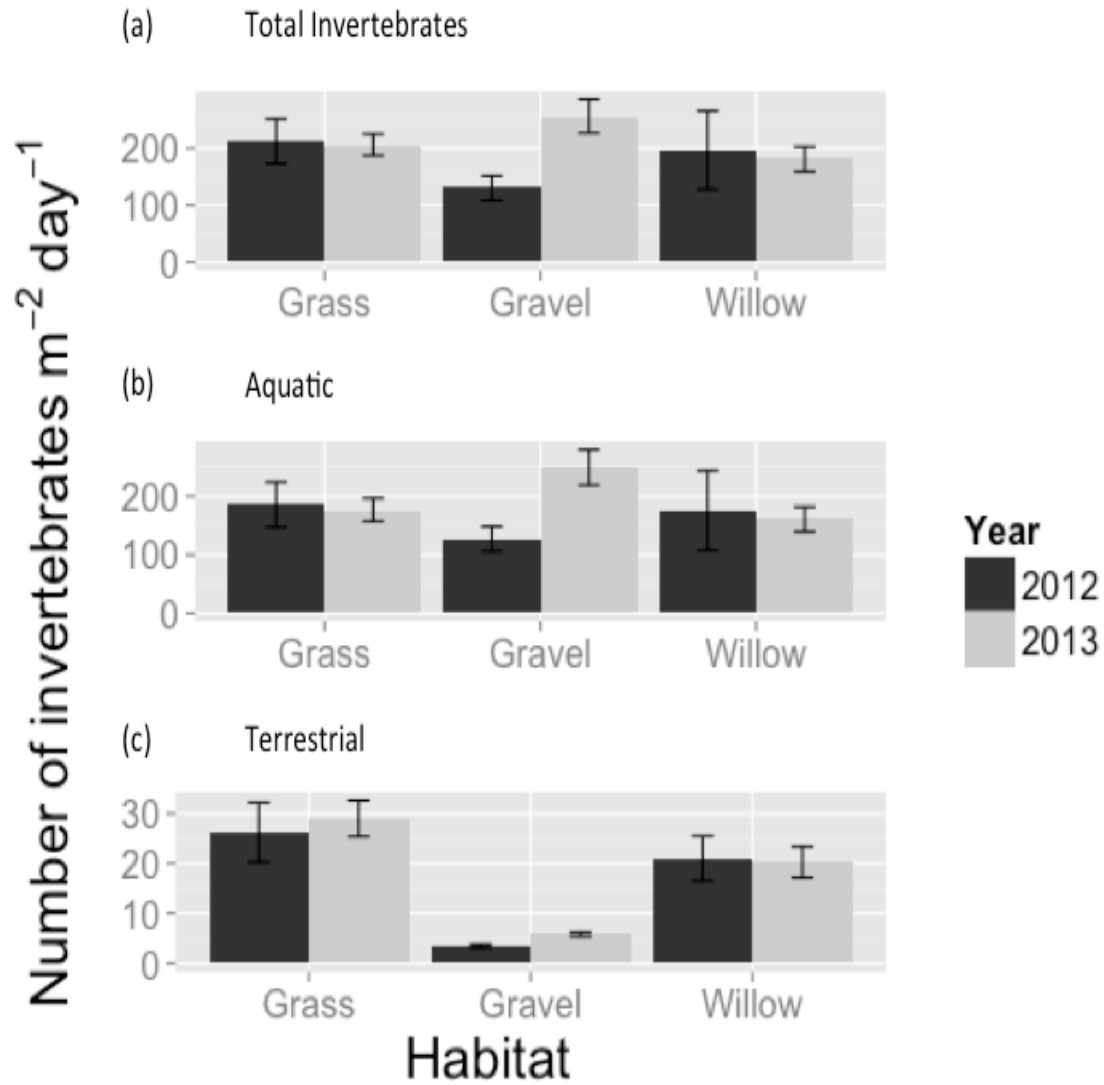


Figure 1.4 Mean (\pm SE) invertebrate abundance (a), adult aquatic insect abundance (b) and terrestrial invertebrate abundance inputs to the Upper Arkansas River Basin from three different habitat categories (grass, gravel, and willow) in 2012 and 2013

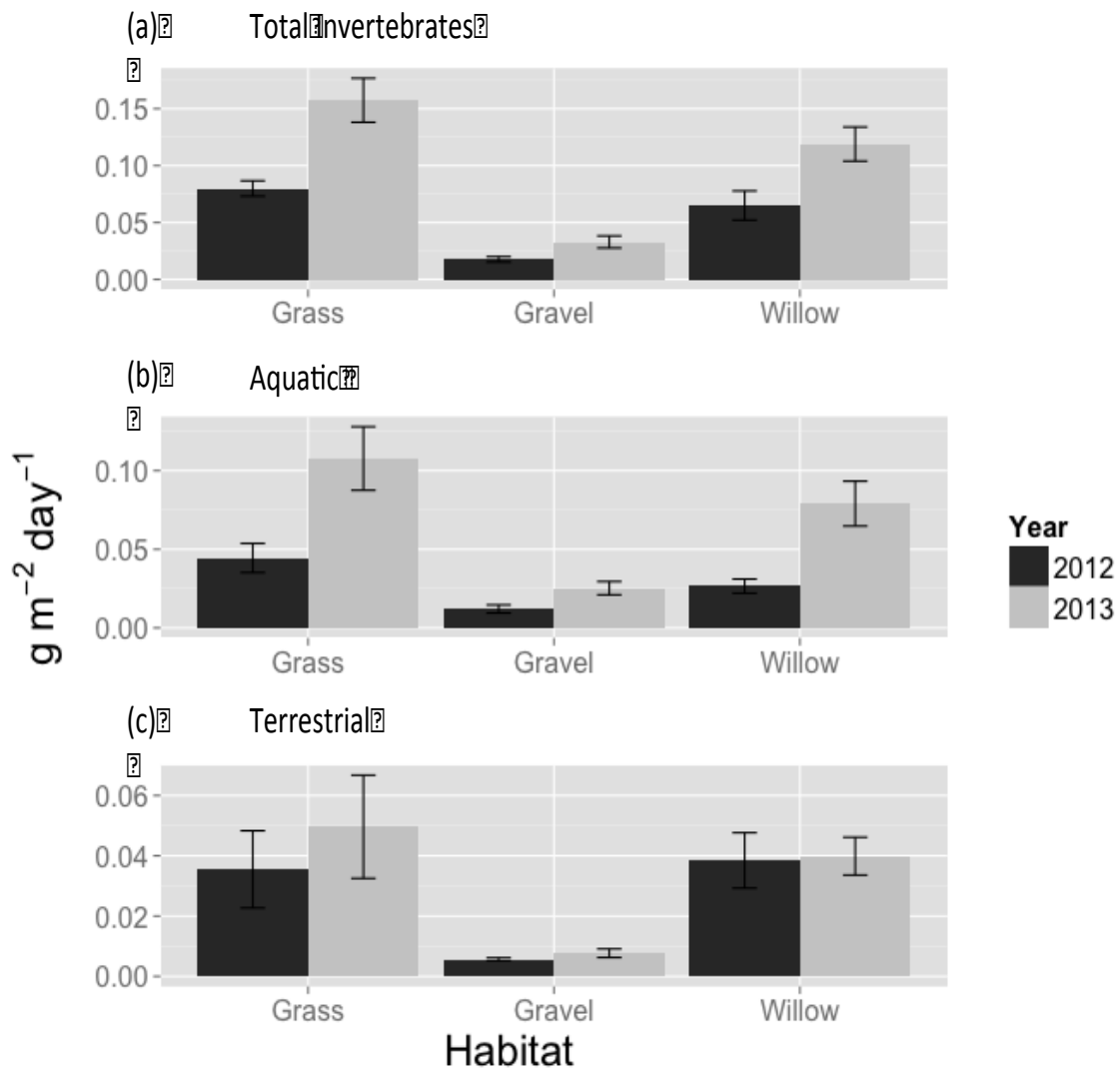


Figure 1.5 Mean (\pm SE) dry weights ($\text{g} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$) of invertebrate inputs from three habitat categories (grass, willow, gravel) at 6 sites along the Upper Arkansas River in 2012 and 2013. (a) Total invertebrate, (b) adult aquatic insects and (c) terrestrial invertebrates, note the difference in scale.

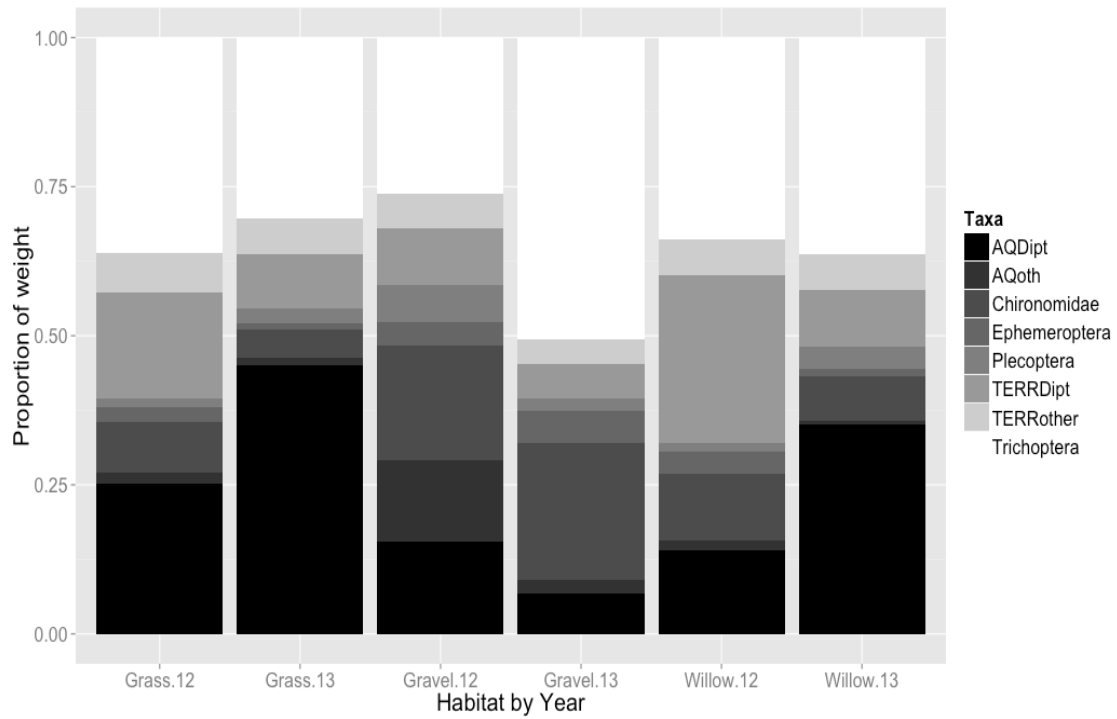


Figure 1.6 Relative contributions of groups to total biomass (dry weight) for three habitat categories (willow, grass and gravel) from the Upper Arkansas River basin in 2012 and 2013.

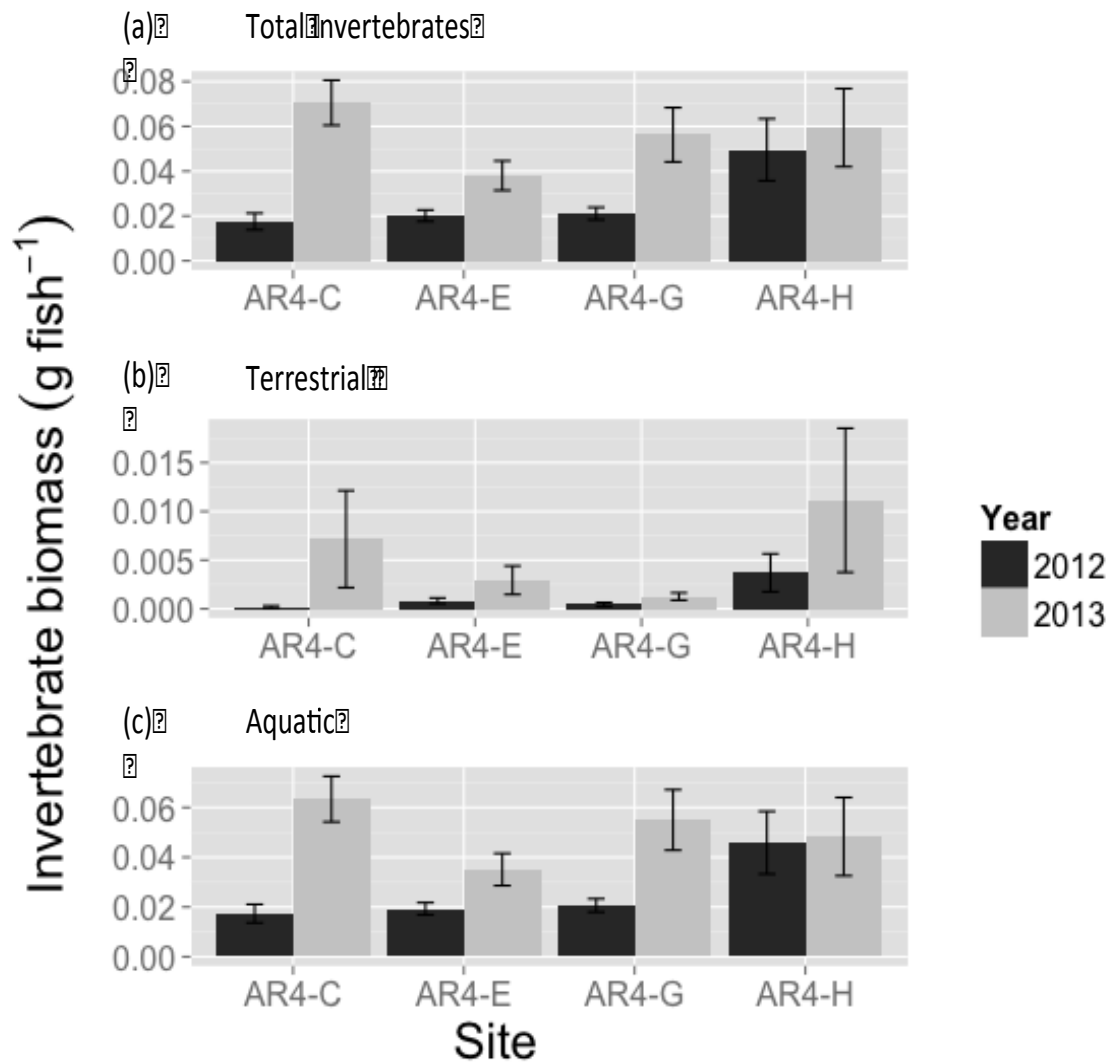


Figure 1.7 Average (\pm SE) brown trout diet biomass (dry weight) from four sites along the Upper Arkansas River Basin in 2012 and 2013. a) total invertebrate biomass, b) terrestrial invertebrate biomass c) aquatic insect biomass

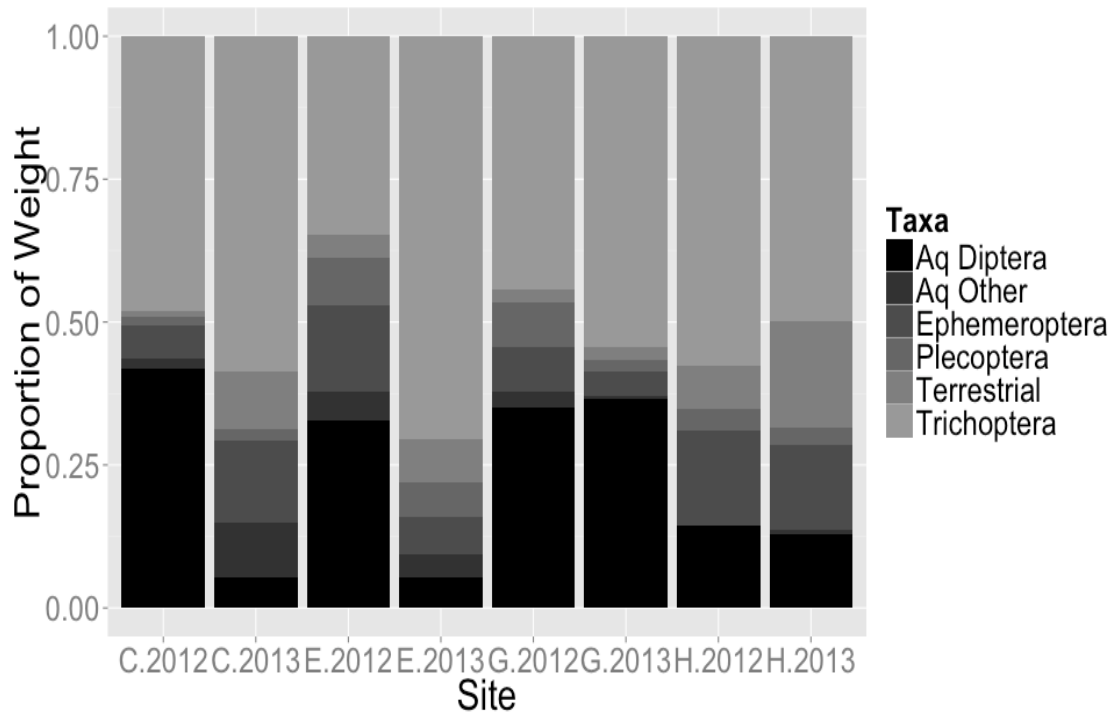


Figure 1.8 Relative contributions of taxa to total dry weight in brown trout diets from four sites along the Upper Arkansas River Basin. Site and year combinations are abbreviated to X.#### for clarity. Aq Diptera = all aquatic dipteran taxa; Aq Other = all other aquatic taxa not represented by the other categories, primarily aquatic Coleoptera and Hemiptera; Ephemeroptera = all mayfly taxa; Plecoptera = all stonefly taxa; Terrestrial = all terrestrial macroinvertebrate taxa; Trichoptera = all caddisfly taxa.

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Chapter 2: Aquatic subsidy export in a fourth order, Rocky Mountain Stream

Introduction

Ecosystem subsidies are defined as nutrients or energy crossing arbitrarily defined boundaries from a more productive donor system to a less productive recipient system (Polis et al. 1997). These subsidies are passive and typically donor-controlled. This differs from active biological connections, such as piscivorous terrestrial consumers, that interact with their prey and have direct feedback loops (Richardson and Sato 2014). Recipient communities of subsidies may benefit through increased productivity, increased consumer densities, or increased growth rates.

Streams have often been viewed as systems with relatively low productivity, requiring energy subsidies from spatially coupled riparian zones to support resident fish and macroinvertebrate communities. Leaf input to streams has been a defining characteristic of lotic ecology for >30 years (Vannote et al. 1980). Leaf litter input often forms the base of the food web (Cummins 1974, Wallace et al. 1997), particularly in low order, eastern deciduous streams with a closed canopy riparian forest.

More recently, emergence of aquatic insects has been shown to provide a resource subsidy to terrestrial consumers (Baxter et al. 2005) that may be disproportionate to the size of the flux. In a year-long study of aquatic insect secondary production and emergence, Jackson and Fisher (1986) found that approximately 97% of the emergent biomass was exported to the riparian corridor in an Arizona stream. Nakano and Murakami (2001) conducted a 14 month study in Northern Japan involving aquatic emergence, and found that adult aquatic insects comprised 26% of the total annual energy budget for 10 bird species. Stable isotope studies have shown that web-spinning and free-living spiders in the riparian zone obtain 68 to 100% of their carbon from aquatic sources (Sanzone et al. 2003).

Emergence has been shown to vary spatially. Iwata et al. (2003) and Iwata (2007) found that emergence from pools was 4.5 times that found in riffle habitats, and attributed the difference to increased abundance of benthic detritivores as well as the increased retention time in pool habitats. Likewise, Power et al. (2004) proposed that any geomorphological feature of streams that retains larvae or provides a predation refuge may increase local emergence. Wipfli and Baxter (2010) likewise point out that trout in pools are often dependent on benthic macroinvertebrates drifting downstream from riffles as a dominant food source.

The timing of aquatic insect emergence has also been shown to vary. Nakano and Murakami (2001) found that emergence was greatest in late spring, when terrestrial invertebrate abundance was low. The timing of this emergence subsidized resident bird species, allowing them to meet their energy demands before terrestrial invertebrate prey abundance increased. They also reported low levels of aquatic emergence throughout the year, and showed that the winter wren, a winter-only resident, received 98% of its diet from emergent insects.

In addition to providing subsidies to terrestrial systems, emerging insects are also an important resource for aquatic consumers. The primary role of most adult aquatic insects is reproduction. After successfully mating, many insects return to the water surface in order to lay their eggs. Some proportion of these insects are consumed by aquatic insectivores such as trout (Saunders and Fausch 2012), and others drown and enter the aquatic detritus pool. When estimating aquatic subsidies being exported to the terrestrial system, it is important to measure the amount of aquatic insects returning to the water surface (Jackson and Fisher 1986). In order to fully characterize aquatic subsidies, it is necessary to measure two endpoints, emergent biomass and biomass re-entering the water column. With these two data points, aquatic subsidy export can be calculated as follows:

$$\text{Emergent Biomass} - \text{Returning Biomass} = \text{Aquatic subsidy export}$$

Few studies have examined the annual variation in aquatic insect emergence and export. Characterizing inter-annual variability is important, especially in lotic systems, which can have a large range of natural variability (Baron et al. 2002, Woelfle-Erskine et al. 2012). Although most work examining the range of natural variability in rivers and streams has focused on flow regime (Poff et al. 1997) or geomorphology (Wohl et al. 2005, Woelfle-Erskine et al. 2012), it is often assumed that biological endpoints will also respond to this variability (Poff et al. 1997, Baron et al. 2002, Wohl et al. 2005). Unfortunately, few papers examine these response variables for more than one year.

I examined benthic population densities and emerging aquatic insect abundances for four years, as well as benthic biomass, emergent biomass and subsequent return to the water surface for two years along the Upper Arkansas River Basin. I chose to estimate abundance and biomass in order to assess the population dynamics of aquatic insects, as well as the amount of dry mass entering the riparian zone. Abundances were estimated in order to understand the annual population dynamics of aquatic insects and biomass was estimated because this is of critical importance for riparian insectivores. This study was initiated as a baseline-monitoring program to assess the effectiveness of physical in-stream restoration activities that were initiated in the fall of 2013.

Methods

Study Site

Seven study sites (AR4.C, AR4.D, AR4.E, AR4.F, AR4.G, AR4.H and AR5) were located along a 4 km reach of the Arkansas River, near Leadville, Colorado. The study area was located approximately 7 km downstream from California Gulch, a historical source of heavy metal contamination to the stream. California Gulch and much of the surrounding watershed was designated as an EPA superfund site in 1983, and chemical and physical restoration continues at

the site. Chemical remediation began in the early 1990's, and water quality has largely improved (Clements et al. 2010). Physical in-stream and riparian habitat restoration began in fall 2013, and this study was initiated to assess the effectiveness of this restoration.

The United States Geological Survey (USGS) measures discharge ($\text{ft}^3 \text{s}^{-1}$) seasonally (May-August) at site AR4.D (USGS Gauge 07083710). Because there are no major tributaries between this gauge and the most downstream site (AR5), this information was used to estimate annual discharge values. Temperature was recorded hourly from October 2011 to August 2013 at the most upstream and downstream sites, AR4.C and AR5, using HOBO V2 WaterTemp data loggers (Onset Computer Corporation, Pocasset, MA). Annual temperatures were averaged between the two sites in order to characterize the annual thermal regime.

Invertebrate Sampling

Benthic macroinvertebrates were sampled from 4 sites (AR4.D, AR4.F, AR4.G and AR5) in mid-August from 2010-2013. Five replicate Hess samples (0.1 m^2) were collected from riffle habitats and stored in 80% ethanol (Clements et al 2010). Samples were sorted in the laboratory, and identified to the lowest practical level of taxonomic resolution (genus or species for most organisms; tribe for chironomids). Samples from 2012 and 2013 were then dried at 60°C for 48 hours to obtain estimates of dry mass (Saunders and Fausch 2012).

Aquatic insect emergence was assessed using 3 floating emergence traps at six sites (AR4.C, AR4.D, AR4.E, AR4.G, AR4.H, and AR5) from 2010-2013. Samples were collected from scour pools along the stream margin for 48 hours twice yearly in August. Previous work has indicated that pools have higher rates of emergence (Iwata 2007, Malison et al. 2010). Floating emergence traps were modified from Malison et al (2010). The same base dimensions (0.33 m^2) were used, but modified the shape to a pyramid and added a collection bottle filled with approximately 200 ml of 80% ethanol. The pyramid shape was employed in order to funnel insects toward the bottle, and

the bottle was added to expedite sample collection. Emergence samples were sorted and identified in the laboratory. Samples from 2012 and 2013 were then dried at 60°C for 48 hours in order to obtain dry mass (Saunders and Fausch 2012).

Plastic pan traps (0.41 m²) were placed along the stream margin in 2012 and 2013 in order to collect adult aquatic insects returning to the water surface. Pans were filled with stream water and approximately 5 mL surfactant to reduce surface water tension. Invertebrates were removed using a small aquarium net and preserved in 80% ethanol. Samples were identified in the lab, and dry mass was assessed after drying at 60°C for 48 hours (Saunders and Fausch 2012).

Statistical Analysis

All statistical analyses were conducted using the program R (R Core Team 2013). Repeated-measures analysis of variance (ANOVA) was used to test for differences in total invertebrate abundances and dry weights based on year and site. All dry weights and abundance data were log transformed in order to satisfy assumptions of parametric statistics. Abundance and biomass data were converted to units per m² per day for direct comparison.

I compared benthic densities to emergence abundances in 2010-2013 in order to estimate a relative proportion of larvae reaching adulthood. This metric is not intended to be an absolute value, or meant to be compared to other systems or studies. Benthic samples provide a single snapshot in time of all instars, cohorts, generations, and taxa present. This becomes even more complicated when considering taxa that are multi-voltine (many generations per year), or semi-voltine (one generation > 1 year). Emergence is highly variable in time, and dependent on water temperature, stream discharge, nutrient availability, etc. The purpose of this metric is solely to compare this system throughout all 4 years. I believe that this is a relevant metric because any biases throughout the study should be similar between years, and this gives us a relative estimate

to qualitatively compare the differences in benthic standing crop and emergence throughout this study.

For 2012 and 2013, I calculated annual emergence biomass and annual aquatic insect biomass returning to the water surface per $\text{m}^2 \text{d}^{-1}$. In order to estimate aquatic insect export to the riparian zone, I subtracted the estimated biomass returning to the water surface from the estimated total emergent biomass. The remainder was assumed to have been exported to the riparian zone (Jackson and Fisher 1986)

Results

Total benthic invertebrate abundances did not differ among sites ($P=0.14108$); however, there were highly significant differences among years ($P<0.0001$) (Figure 2.1). Total macroinvertebrate abundance across all stations significantly increased in 2013 compared to other years. Relative taxonomic composition of benthic communities was also similar between years, except for a decrease in 2013 of Ephemeroptera and an increase in Diptera (Figure 2.2).

Benthic biomass did not differ spatially ($P=0.36768$), but was significantly different between years ($P=0.0014$, Figure 2.3). Interestingly, benthic biomass decreased in 2013 by 31% compared to 2012. This differs from the benthic abundance which increased in 2013. Additionally, the benthic composition in 2013 was dominated by small chironomid larvae, and showed a decrease in large bodied Plecoptera and Ephemeroptera.

Emergence of adult aquatic insects did not differ among sites ($P=0.3143$), but there was significant annual variation, with increased emergence in 2011 and 2012 ($P=0.0002$, Figure 2.4). Relative taxonomic composition of emergence was dominated by Diptera (65-89%) and Trichoptera (10-28%) (Figure 2.5).

The ratio of total emergence to total macroinvertebrate abundance in the benthos was similar in all years except 2013, which showed a marked decrease (Figure 2.6). This is due to the

dramatic increase of abundance in the benthos and a slight decrease of emergence in 2013 (Figure 2.1).

The emergent biomass showed no variation among stations ($P=0.7202$), but did increase by a factor of 1.6 in 2013 ($P=0.0080$). Likewise, there was an increase of 2.5 times in the input of adult aquatic insects in 2013. The percentage of emergent biomass that was found in the pan traps was 30 and 50% in 2012 and 2013 respectively, representing an estimated export of 0.0257 and 0.0673 g per m² per day from the stream to the riparian habitat (Figure 2.7). This shows considerable annual variation in cross ecosystem subsidies, and highlights the importance for measuring numerous endpoints when conducting food web studies.

Discussion

I found that benthic invertebrate abundances, emergent abundance and biomass, as well as aquatic biomass export to the riparian zone was similar throughout the restoration reach, but varied significantly on an annual basis. The similarity among stations was not unexpected. All stations are located relatively close together, and have similar abiotic and biotic factors. It is likely that the spatial component will become a more important factor post-restoration, as some of these sites will be directly restored. Additionally, this provides us with a robust pre-restoration data set in order to make appropriate conclusions.

Total benthic abundances were similar in all years except 2013, which was nearly double the average for the preceding three years. This increase was largely due to Diptera abundances increasing by 2.5 times the average of the previous 3 years. Likewise, the abundances of Trichoptera increased in 2013, while the abundances of Ephemeroptera and Plecoptera were reduced.

Potential mechanisms that could explain the drastic change in benthic abundance in 2013 compared to other years include differences in flow and temperature regimes. The winter of 2011-

2012 was characterized by a very low snowpack and the summer of 2012 was hot and dry, resulting in an extremely low annual discharge (Table 2.1). Additionally, water temperature was slightly higher in 2012, as is typical in low flow years (Todd et al. 2008). Unfortunately I only have temperature data for 2 years, so cannot say anything definitive about thermal regimes in this system. It is possible that these conditions stressed the more sensitive taxa (Ephemeroptera and Plecoptera), while the more tolerant taxa (Diptera and Trichoptera) were able to tolerate these conditions. Indeed, emerging insects in 2012 were dominated by Trichoptera and Diptera. If the Trichoptera and Diptera had higher probabilities of survival to emergence in 2012, they would also have been more likely to lay more eggs in 2012, explaining the increase in abundance in the benthos in the ensuing year.

Total emergent abundances also changed annually, but this did not follow the same pattern and was not as pronounced. This may be more due to the inherent variability of emergence sampling. Many aquatic insects display synchronous emergence over a short time period, depending on thermal and flow regimes, nutrient availability, etc., making robust estimates of emergence difficult without numerous samples (Jackson and Fisher 1986, Malison et al. 2010). Additionally, sampling emergence from floating emergence traps in pools often underestimates emergence of taxa that crawl out on the bank to emerge (e.g., Plecoptera and some Ephemeroptera). Other studies have placed traps half-on the bank and half-on the water in order to correct for this bias (Malison et al. 2010). The sites along the Arkansas River are predominantly incised, and I was unable to find suitable locations at all sites to place traps half-on the bank. However, in a pilot study of emergence conducted in 2012 sampling numerous fluvial habitats throughout summer at one site, I found that most Plecoptera emerge in June and July, and the annual estimates of August emergence from pools is similar to that found in other habitats (Pomeranz, unpublished data). Thus, I believe that this sampling scheme is representative of the emergence in August, and is comparable among years.

The ratio of emergence to benthic abundance was very low (0.8 to 2.7%) in this study, but this was not unexpected. Benthic sampling collects individuals from all generations and instars present at that time, whereas emergence sampling only collects those individuals that emerge during a relatively short time interval. The fact that the emergence ratio was similar in 3 of the 4 years suggests that this is an appropriate estimate of emergence for this system at this time of the year. Additionally, the year with the lowest proportion of emergence (2013) also had dramatically elevated levels of benthic invertebrate densities and low (although still comparable) levels of emergence. It is unclear why there was such an increase in benthic densities from 2012 to 2013. One hypothesis is that the reduced flow in 2012 allowed more food and nutrients to be stored throughout the reach, and there was subsequent increase in benthic population densities. Additionally, water temperatures in 2012 were elevated compared to 2013, but since temperature data from the previous 2 years is unavailable, this information may be misleading. Further multi-year studies are needed to investigate this potential lag effect of reduced flow on benthic densities.

An estimated 0.0855 and 0.1346 g per m² per day emerged from the Arkansas River in 2012 and 2013, respectively. These values are similar to estimates of emergence flux in other studies (Jackson and Fisher 1986, Kato et al. 2003, Sanzone et al. 2003, Iwata 2007, Malison et al. 2010). I estimated that 30-50% of the emergent biomass returned to the water surface in 2012 and 2013, resulting in an export of 0.03-0.07 g per m² per day (Figure 2.7). This is much lower than the 97% of emergent biomass exported to the riparian zone in an Arizona stream (Jackson and Fisher 1986). It is likely that this estimate is much lower due to the shorter growing season of the Arkansas River and reduced growth rates of benthic macroinvertebrates in this high elevation, cold, mountain stream, versus their low elevation, warm, desert stream. However, this is the only study that I am aware of that estimated the proportion of emergence to return to the water surface, so is the only point of comparison currently available. This estimate also only includes aquatic biomass exported in August, and it is likely that total annual exports are higher, as emergence is generally higher in

late spring and early summer (Iwata et al. 2003, Baxter et al. 2005, Iwata 2007, Malison et al. 2010). Indeed, during a pilot study conducted in 2012, I found emergence in July to be higher than those in August, but both of these months had greater emergence magnitudes than June. Biomass of these samples was not measured, so a direct comparison cannot be made (Pomeranz, unpublished data). It is likely that the high elevation and low annual average temperatures shift peak emergences in this system from late spring / early summer to late summer / early fall.

These results also highlight the importance for measuring multiple endpoints in studies of ecosystem subsidies. For example, if only emergence was measured, one would conclude that the aquatic subsidy in 2013 was the lowest of all 4 years sampled. When the biomass data is incorporated, which is more relevant to riparian consumers, I showed that the net biomass actually increased in 2013 by a factor of 1.6. Finally, when the aquatic insect biomass returning to the stream is subtracted from the total emergent biomass, this provides a more realistic estimate of true aquatic biomass export.

As previously discussed, aquatic subsidies provide seasonal resources to riparian insectivores such as birds, bats, spiders, and lizards (Baxter et al. 2005). It is estimated that 1 g dry mass of adult aquatic insects contains 24.8 kJ of energy (Cummins and Wuycheck 1971). Therefore, an estimated 0.744 – 1.73 kJ of energy was exported to the riparian habitat per m² per day in August 2012 and 2013, respectively.

This study also highlights the importance of measuring annual variability in ecosystem processes. Many ecosystem processes have a natural range of variability, and may go through complex interactions and cyclical phases. In addition, there may be time lags between response variables. For example a mesocosm experiment manipulating fish density found that fish predation reduced benthic standing crop, but that this effect was dampened in emergence values (Wessner 2013). Measuring several endpoints in multiple years will help researchers and managers properly

assess changes and trends in ecosystem processes and services, and make appropriate decisions based on this information. With that in mind, it is important to continue monitoring this system for multiple years post restoration activities, in order to fully characterize the restoration effectiveness.

Tables and Figures

Table 2.1. Annual mean temperature ($^{\circ}\text{C}$) and annual discharge (Q , $\text{ft}^3 \text{s}^{-1}$). Temperature values were recorded at AR4.C and AR5 and averaged between the two sites. Temperature was not recorded in 2010 and only October-December in 2011. Temperature was recorded from January-December in 2012, and January-August 2013. Discharge values are from USGS gauge 07083710 which operates from May to August, annually.

Year	Temperature	Q
2010	--	269
2011	--	600
2012	6.2	113
2013	5.5	227

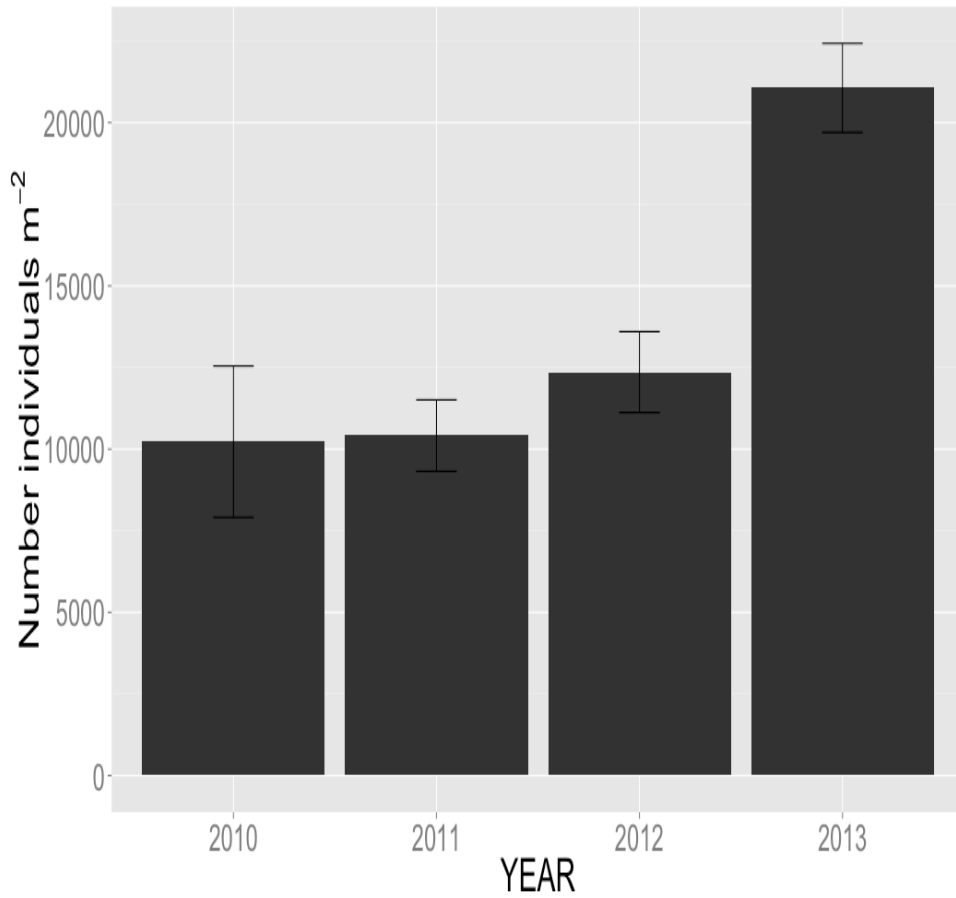


Figure 2.1. Mean (\pm SE) number of individuals per m^2 in the benthos from 4 sites in the Upper Arkansas River Basin, from 2010-2013.

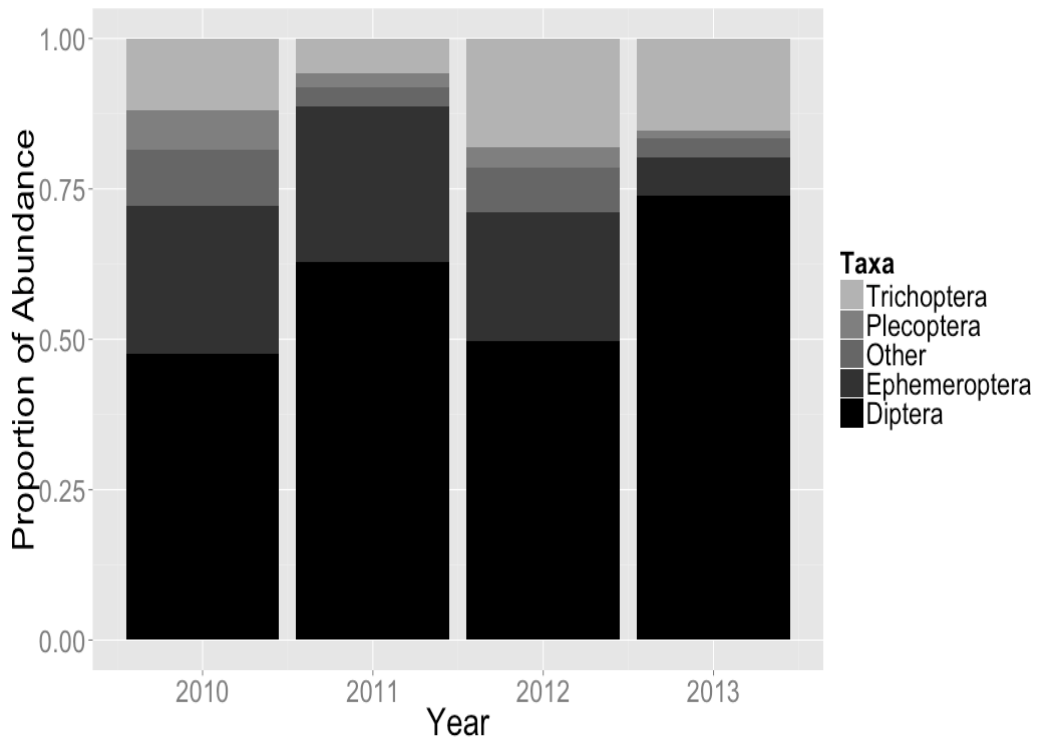


Figure 2.2. Relative contribution of aquatic orders to the benthic community from 4 sites in the Upper Arkansas River Basin, from 2010 to 2013. Other is primarily aquatic Coleoptera and Hemiptera.

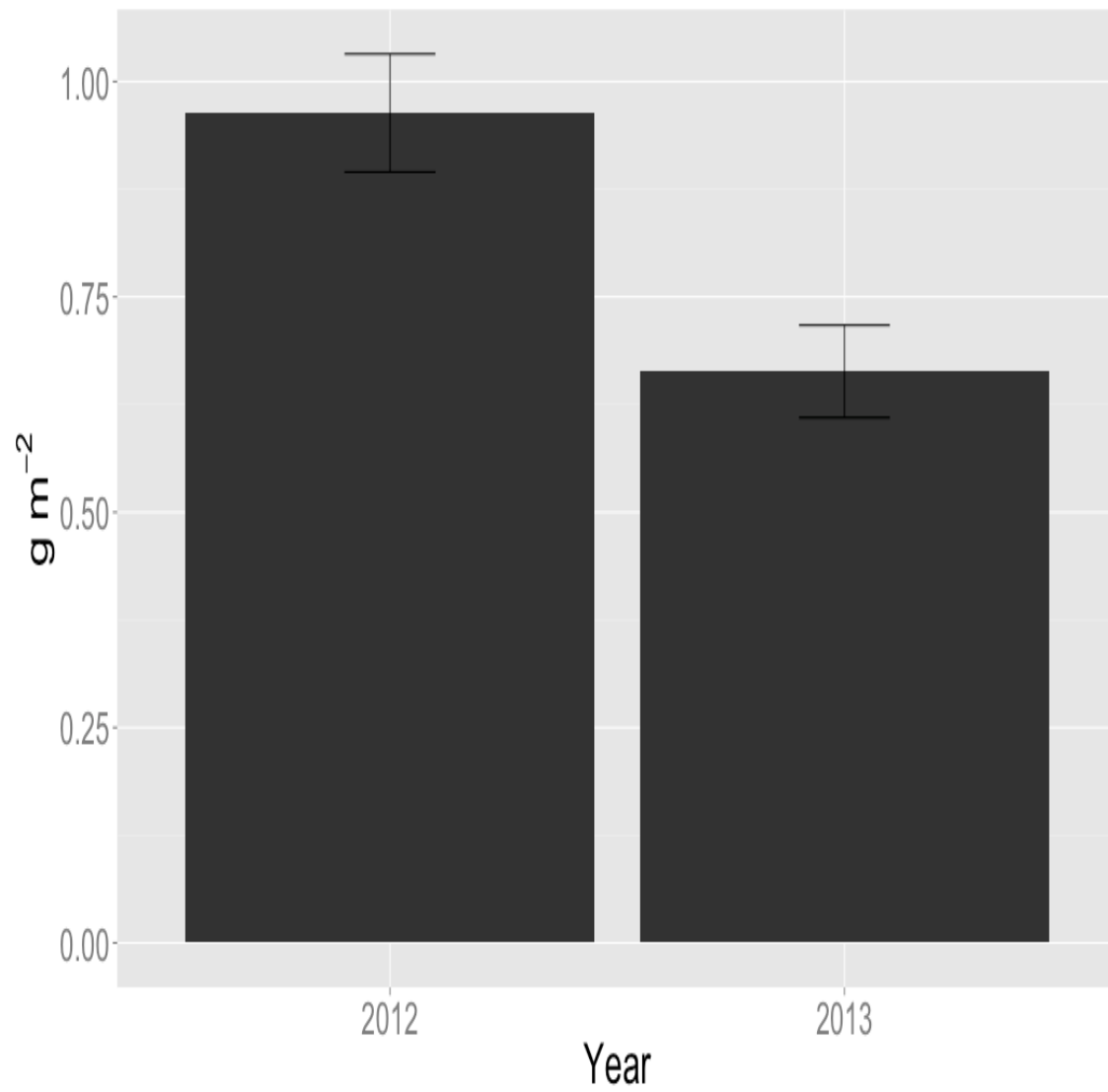


Figure 2.3. Mean dry mass (\pm SE) of benthic macroinvertebrates from 5 sites along the Upper Arkansas River Basin in 2012 and 2013.

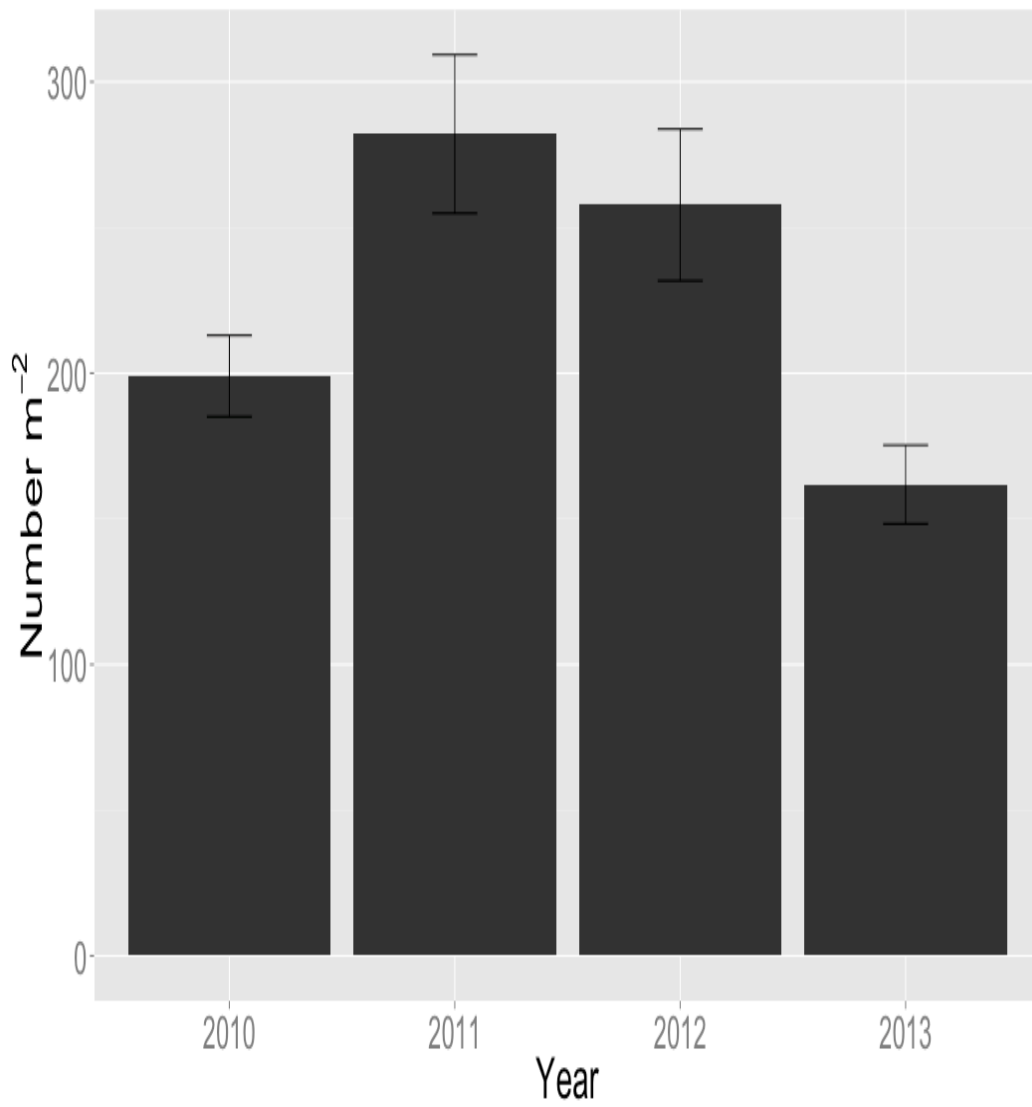


Figure 2.4. Average (\pm SE) number of emergent aquatic insects per m² from six sites along the Upper Arkansas River Basin, from 2010-2013.

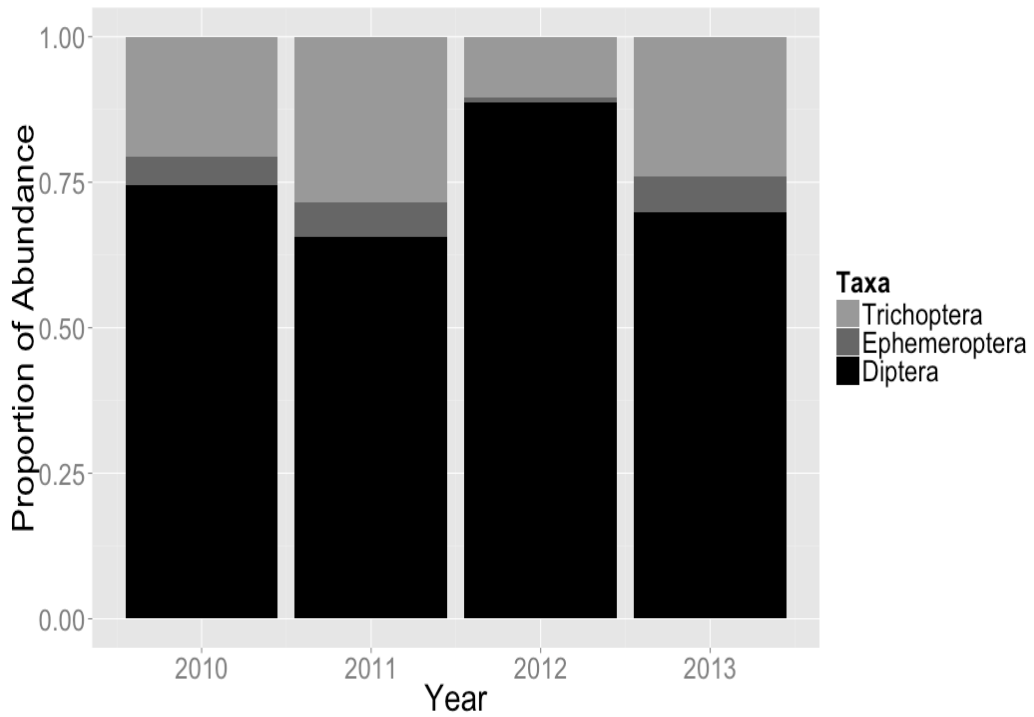


Figure 2.5. Relative contribution of Trichoptera, Ephemeroptera and Diptera to total emergence from six sites along the Upper Arkansas River Basin, from 2010-2013. Emergent Plecoptera, which contributed <1% in all years, are not displayed.

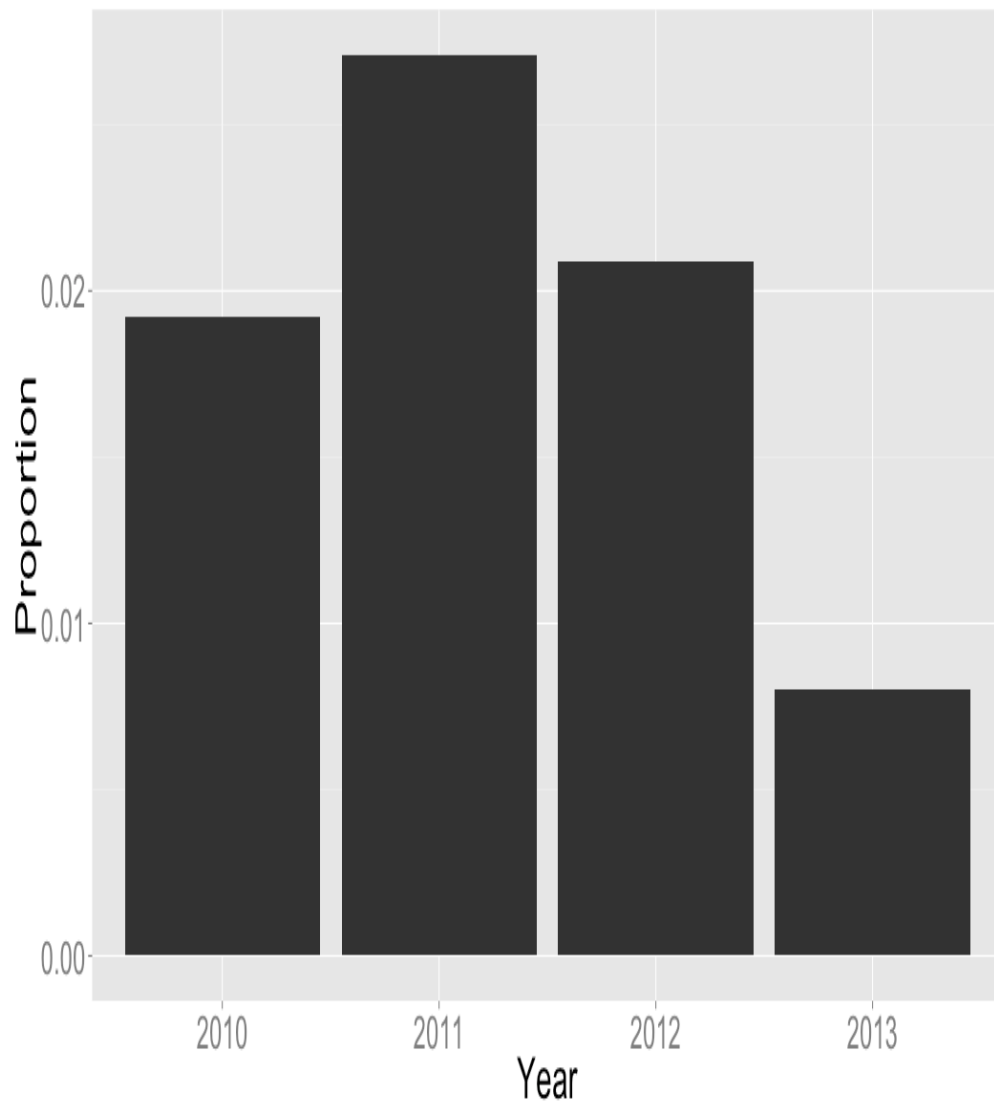


Figure 2.6. Proportion of individuals in the benthos that successfully emerged from six sites located along the Upper Arkansas River Basin, from 2010-2013.

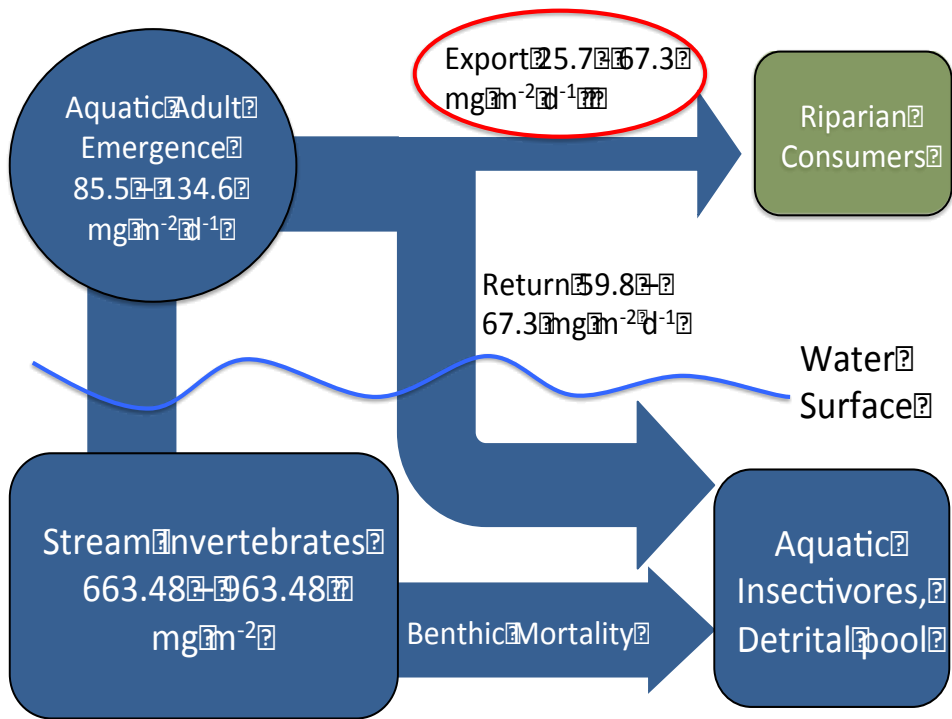


Figure 2.7. Conceptual model summarizing the flow of invertebrate subsidies from the aquatic system to the riparian zone along the Upper Arkansas River Basin. Numbers represent the average dry mass ($\text{mg m}^{-2} \text{d}^{-1}$) in 2012 and 2013 respectively.

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