Understanding Benthic Macroinvertebrate Communities in Beaver Meadows of Rocky Mountain National Park

By Valerie T. Doebley
Colorado State University

Abstract

In mountain regions, river-floodplain meadows can develop in unconfined valley sections of the river network. River-floodplain meadows are ecologically significant regions due to their ability to retain carbon and nutrients through several processes, including the storage of large woody debris and the accumulation of particulate and dissolved organic carbon in the sediment during flood events. These processes are influenced by the historic land use, such as livestock grazing or farming, and the presence of beavers in the meadow. Past projects in Rocky Mountain National Park examined the physiochemical and hydrologic characteristics of river-floodplain meadows with current or past beaver activity. However, past studies did not look at the communities of aquatic organisms residing in these areas.[1,2] Aquatic macroinvertebrates are an effective biological indicator that are used to examine the effects of anthropogenic impacts on lotic ecosystems. The purpose of this study is to examine the aquatic macroinvertebrate communities at the inflows and outflow of six beaver meadows of Rocky Mountain National Park. By studying the aquatic insect communities at both ends of active and abandoned beaver meadows, this project examines: 1.) How the location above or below a meadow impacts communities, by comparing community composition at the outflows to inflows of meadows; 2.) any non-location-specific impact of beaver activity by comparing active and abandoned meadow communities, and, 3.) the interaction between location and beaver activity, in other words, a comparison of the change between inflow and outflow communities in active versus abandoned meadows. There were significant differences in several taxa between inflows and outflows of meadows, suggesting that meadows do impact the downstream communities. There were also more families that displayed overall higher abundances in active than abandoned meadows, regardless of inflow or outflow location. There were also two families, Glossosomatidae and Leptophlebiidae, which displayed an interaction effect such that their abundance significantly increased between the inflow and outflow of active meadows, but not of abandoned meadows.

Introduction

River-floodplain meadows in unconfined valley sections of mountain stream systems are an important sink in the carbon cycle.[1] These areas are often impacted by human land-use practices, which can alter the natural dynamics of the river and meadow. The presence or absence of beavers is an important characteristic of river-floodplain meadows that is impacted by past and current land-use practices. Beaver activity is associated with increased geomorphic complexity, carbon retention, and aquatic ecosystem metabolism.[2] Another study found that the river-floodplain meadows with beaver activity are particularly effective at retaining and processing carbon due to several natural processes occurring in these meadows. These processes include the storage of large woody debris and the capture of dissolved and particulate organic carbon into sediments during flooding in unconfined sections.[1] The increased geomorphic complexity, aquatic ecosystem metabolism, and carbon retention in beaver meadows may impact downstream habitat and community composition of biological indicator organisms such as benthic macroinvertebrates.

Examining the macroinvertebrate communities of streams is commonly used to biomonitor how humans impact stream health and water quality.[3] A healthy stream is capable of supporting a diverse macroinvertebrate community with a variety of life history traits and feeding habits. Accordingly, abundance and diversity of macroinvertebrate taxa are biological indicators of stream ecosystem health. Comparing the macroinvertebrate communities of beaver-less meadows with more intense land-use histories to less impacted active beaver meadows can indicate how human activities affect stream quality in meadows.

Furthermore, a stream's characteristics impact the macroinvertebrate community composition due to the various habitat needs and trophic relations of different taxa.[4] The functional feeding groups of the taxa found in a stream can provide insight to the stream's ecosystem and water quality. Since feeding groups such as shredders, collector-filterers, and collector-gatherers rely on coarse particulate organic matter (CPOM) and fine particulate organic matter (FPOM) as food, it is possible that a meadow's effect on the particulate organic carbon in a stream is a mechanism impacting downstream macroinvertebrate community composition.[5]

The purpose of this study is to use benthic macroinvertebrate communities as a lens to examine the differences between the quality of streams at the inflows and outflows of six river-floodplain meadows in Rocky Mountain National Park (RMNP). Based on past studies on the physiochemical and hydrologic properties of river-floodplain meadows[1,2], I hypothesized that macroinvertebrate abundance and diversity would be greatest at the outflows of active beaver meadows. The six meadows in this study were selected because they have different land-use histories and consequently they have different levels of beaver activity and geomorphic complexity. These meadows were also selected because previous studies through Colorado State University's Natural Resource Ecology Laboratory already examined their physiochemical and hydrologic characteristics.[1,2] By examining these meadows at both inflows and outflows, it can be determined if processes occurring within these meadows are impacting the downstream macroinvertebrate communities. Furthermore, comparing the differences between inflows and outflows across active and abandoned beaver meadows can provide insight to the effects of current beaver activity and channel complexity on ecosystem and habitat quality.

Methods

A conceptual diagram outlining the research process for this study is in **Table 1**.

Study Location

Benthic macroinvertebrate sampling was performed at two places on six meadows in Rocky Mountain National Park, for a total of 12 sampling locations. These meadows were divided by activity level into two categories: active meadows and abandoned meadows. Active meadows have current beaver activity and included Mill Creek and Glacier Creek. Abandoned meadows no longer have any beaver activity and included Moraine Park, Upper Beaver Meadows, Hidden Valley and Cow Creek. All of the abandoned meadows had historic beaver activity and still share varying characteristics of active meadows, such as slowed movement of water.

Each meadow was sampled at two locations: an inflow location upstream of the meadow and an outflow location downstream from the meadow (**Figure 1**). Each meadow has one inflow and one outflow. Active meadow sampling locations are referred to as "active inflow" and "active outflow". Abandoned meadow sampling locations are referred to as "abandoned inflow" and "abandoned outflow". Classifications of the six meadows are shown in **Table 2**. Aquatic macroinvertebrates were sampled at both inflow and outflow of each meadow to help determine if processes occurring within a meadow result in differences between the macroinvertebrate communities upstream and downstream of the meadow. The final study design consisted of two active and four abandoned meadows, each with an inflow and outflow sampling location (**Figure 2**).

Field Methods

Benthic macroinvertebrate sampling was performed using a 500-micron Surber sampler and a 600-micron sieve. At each sampling location, Surber samples were collected in riffles or runs no deeper than knee height. Four replicates were taken at four suitable riffles or runs positioned closest to the stream gauging station at each location. Replicates were taken moving from downstream to upstream to avoid disturbing subsequent replicates. At each selected riffle or run: 1) the Surber sampler was positioned, 2) each rock and piece of cobble in the square plot was picked up and vigorously scrubbed by hand so that the contents of the plot flowed into the net, and 3) any remaining sand, gravel, plants, or small rocks within the plot were stirred by hand.

After the entire contents of the plot were thoroughly scrubbed and stirred up, the Surber sampler was removed from the water. The sample was deposited into a five-gallon bucket of water by turning the net of the Surber sampler inside out and dipping it into the bucket. The contents of the bucket were then poured through a 600-micron sieve and transferred into a 1 L plastic jar. The Surber sampler, bucket, and sieve were inspected for any remaining macroinvertebrates, which were transferred into the jar using forceps. Samples were preserved in a 95% ethanol solution. Although lower concentrations of ethanol are adequate to preserve samples, 95% ethanol is used in the field because a small amount of water from the stream ends up the jar, diluting the ethanol's concentration. Once in the laboratory, individual specimens from the sample can be safely transferred into new vials containing an 80% ethanol solution.

Laboratory Methods

In the laboratory, all macroinvertebrates were removed from the sample jars containing 95% ethanol, sorted, and placed into new, separate vials containing 80% ethanol. Other organic materials from the sample were also preserved. All macroinvertebrates from the samples were sorted by taxa using a dissection microscope. Aquatic insect larvae from the samples were sorted by family. Pupas found in the samples were sorted by order. Some samples also included some organisms other than aquatic insects. These included Bivalves, Trombidiformes (water mites), Gastropods, Annelids, Collembola, and terrestrial insects.

Data Analysis

Data analysis was performed using R-studio. A series of one-way and two-way ANOVAs were run to compare the abundance of different taxa across different site categories: active vs abandoned meadows, inflow vs outflow locations, or an interaction (activity level x location), using an alpha-value of 0.1. P-values of less than 0.1 indicate that the difference in abundance between site categories is significantly significant. A p-value greater than 0.1 indicates that there is no significant difference in abundance between site categories. No significant difference could mean: 1.) the site category does not impact the abundance, or 2.) there was not enough data collected to find an impact on abundance statistically significant. For this study, four replicate samples were taken at 12 sites, categorized into two activity levels and two locations. While a greater number of replicates and sites might lead to more statistically significant results, it is still possible to achieve statistically significant results with a relatively small number of sites, especially in cases where there is a strong and consistent relationship between abundance and site category.

For these analyses, the insects were grouped by order, family, or functional feeding group (**Table 3**). Functional feeding groups were determined using information provided in "The Aquatic Insects of North America".[6] All abundance values were logarithmically transformed by taking the natural log of the abundance plus one. Logarithmic transformations are a common way to account for the issue that benthic macroinvertebrate datasets are usually not normally distributed and do not meet the assumptions of parametric statistical methods (e.g., homogeneity of variance).[7]

Results

Total macroinvertebrate abundances were variable between locations, meadows, and in some cases between replicates, with densities ranging from 12 to over 600 specimens per Surber sample. The average abundance of macroinvertebrates per Surber sample in active meadows was 94 specimens at inflow sites and 197 specimens at outflow sites. In abandoned meadows on average there was 111 specimens at inflows and 110 specimens at outflows (**Figure 3**). The number of families of aquatic insects per sample was also examined. Active meadows averaged 9.0 families at inflows and 9.9 families at outflows. Abandoned meadows averaged 8.9 families at inflows and 9.1 families at outflows (**Figure 4**). Neither total abundance nor number of families per Surber sample was found to be statistically significantly different between inflows and outflows or across activity levels.

Macroinvertebrate samples contained aquatic insect larvae from five orders: Ephemeroptera (mayflies), Plecoptera (stoneflies), Trichoptera (caddisflies), Diptera (true flies), and Coleoptera (beetles). These orders are divided into families. The raw data by orders and families can be found in table 4. Three of the aquatic insect orders, Plecoptera, Ephemeroptera, and Coleoptera, were overall more abundant in active meadows than abandoned meadows, regardless of the location on the meadow (p-values = 0.063, 0.0608, and 0.00364, respectively). No orders showed significant differences between inflow and outflow abundances or an interaction effect between activity level and location. Although most of the organisms collected were aquatic insects, some samples also contained Bivalves, Trombidiformes (water mites), Gastropods, Annelids, Collembola, and terrestrial insects.

The aquatic insect larvae found in these samples belonged to several functional feeding groups including collector-gatherers, collector-filterers, shredders, scrapers, herbivorous piercers, and predators (**Figure 5**). In meadows of both activity levels (active and abandoned) and at both locations (inflow and outflow) the most abundant feeding group was collector-gatherers, which accounted for more than half of the total insects collected during this study. The feeding habits of individual families can be found in **Table 3**, as well as the ANOVA results regarding each family.

Collector-Filterers

One noteworthy feeding group was the collector-filterers. For both active and abandoned meadows, the average number of collector-filterers was greater at the meadow's outflow than the inflow (p-value = 0.0731). Families of collector-filterers were Simuliidae, Hydropsychidae, and Brachycentridae. The dipteran family Simuliidae, which accounted for the majority of the collector-filterers, displayed the same pattern as the overall collector-filterer group between the inflows and outflows (p-value = 0.0447). The abundance of Simuliidae likely influenced the overall pattern for its entire feeding group.

The other two families of collector-filterers, Brachycentridae and Hydropsychidae, are both caddisflies and were less abundant than Simuliidae. Neither Brachycentridae nor Hydropsychidae were found to have significant differences in inflow and outflow abundance. However, Brachycentridae was significantly more abundant overall in active meadows than in abandoned meadows, when inflow and outflow abundances are averaged for each meadow. (p-value = 0.000436). The opposite was true of the family Hydropsychidae, which was significantly more abundant in abandoned meadows than in active meadows, regardless of the location on the meadow (p-value = 0.0863).

Collector-gatherers

The collector-gatherer feeding group contained the majority of aquatic insects in this study. While the collector-gatherer group overall did not have any differences between inflows and outflows or between activity levels, individual families within the group displayed some significant results. A collector-gatherer mayfly, Leptophlebiidae, had a significant interaction between location and activity level (p-value = 0.0680), in which the abundance was found to increase between inflow and outflow in the active meadows, and decrease between inflow and outflow in the abandoned meadows. Leptophlebiidae was also more abundant at the inflows than the outflows of meadows of all activity levels (p-value = 0.0774). Two other collector-gatherer families were significantly more abundant in active meadows than abandoned meadows, regardless of inflow or outflow location; these families were Baetidae (p-value = 0.00757), and Elmidae (p-value = 0.0034).

Piercers

The feeding group piercers were found almost exclusively at abandoned meadows. The caddisfly Hydroptilidae was the only piercer family present in this study. This family was found to be significantly more abundant at abandoned meadows than active meadows (p-value = 0.0539).

Predators

While the predator feeding group overall did not produce any significant results, individual families within the predator group displayed some significant results. One such predator was the stonefly Chloroperlidae, which was more abundant in the active meadows than the abandoned meadows, regardless of inflow or outflow locations (p-value = 0.0477). Another predacious stonefly, Perlidae, displayed an interaction effect between activity level and location in which their abundance was significantly higher at the active inflow than any other site (p-value = 0.0423). A predacious dipteran, Dolichopodidae, displayed they same interaction behavior as Perlidae (p-value = 0.0126). Additionally, Dolichopodidae was significantly more abundant at inflows than outflows, regardless of the meadow's activity level (p-value = 0.0725). Although these results are statistically significant, it's important to consider that only six total Dolichopodidae specimens were found during this study, and all six were found at the inflow to Mill Creek, an active beaver meadow.

Scrapers

The scraper feeding group also displayed several interesting differences in distribution across the meadows. For both active and abandoned meadows, the average number of scrapers was greater at the meadow inflow than the meadow outflow (p-value = 0.0008). The families of scrapers included Heptageniidae, Ameletidae, Uenoidae, and Glossosomatidae. The scraper mayfly Heptageniidae was found to be significantly more abundant at the inflows than the outflows for meadows of both activity levels (p-value = 1.29E-05). Because Heptageniidae was a very abundant scraper family, Heptageniidae influenced the overall patterns seen in the distribution of scraper feeders.

In addition to Heptageniidae, there were several less abundant scraper families. Another scraper mayfly family, Ameletidae, was significantly more abundant in active meadows than abandoned meadows (p-value = 0.0301). It is worth noting that Ameletidae was very uncommon in this study and was only present at one active meadow, Hidden Valley, and one abandoned meadow, Cow Creek. The family Glossosomatidae is a scraper caddisfly which had a significant interaction between location and activity level (p-value = 0.0691), in which the abundance was found to increase between inflow and outflow in the active meadows, and decrease between inflow and outflow in the abandoned meadows. Another scraper caddisfly family, Uenoidae, was only found three times during this study, twice at the inflow of an active meadow, Mill Creek, and once at the outflow of an abandoned meadow, Hidden Valley.

Shredders

The only shredder feeder that produced significant results was the stonefly Nemouridae. Nemouridae was significantly more abundant overall in active meadows than in abandoned meadows (p-value = 0.0569). While not statistically significant, Nemouridae also behaves as though it may have an interaction between inflow/outflow and activity level (p-value= 0.1243). Nemouridae was the most abundant shredder family from this study and influenced the overall patterns seen in the distribution of shredder feeders. Large amounts of variation between replicates caused the interaction for Nemouridae to not be statistically significant, even though in figure 5 this interaction appears quite drastic for shredders. The collector-gatherer Elmidae also showed the same insignificant pattern as Nemouridae, in which abundance appears to increase more between the inflow and outflow of the active meadows than the abandoned meadows. Although not always significant, the presence of this same pattern across several taxa should be noted due to the possibility of it not being due to random chance.

Discussion

The results of this study can be grouped into three categories regarding the macroinvertebrate community composition: differences across inflows and outflows, differences across active and abandoned meadows, and an interaction effect of these two factors. First, differences in the abundances of several taxa across inflows and outflows, regardless of meadow type, suggest that processes occurring within floodplain meadows are altering the downstream aquatic insect communities. Second, some taxa are more abundant in active meadows overall, regardless of inflow or outflow location, suggesting that some characteristic of study areas are affecting the streams upstream of the meadows as well as downstream of the meadows. Finally, for some taxa an interaction occurs in which active meadows have different changes between the inflow and outflow communities than abandoned meadows. This interaction suggests that some aquatic insect taxa are more sensitive to differences between active and abandoned meadows and the processes occurring within them that impact outflow habitat. The mechanisms causing these three different categories of results are not directly examined in this study. Information from past publications on the feeding habits and life history traits of different aquatic insects can help predict possible mechanisms driving these differences in aquatic insect communities.[8,9]

Differences between inflows and outflows

For some families, their average abundance was significantly different between inflows and outflows. The families in **Figures 6 and 7** demonstrate examples of this type of relationship. Due to their location, outflow habitats are subject to the ecological impacts of processes occurring in the meadows upstream, while inflow habitats are not. Meadow processes include storage and gradual breakdown of woody debris, capture of nutrients such as organic carbon in sediments during flood events, and a slowed movement of water through unconfined valley segments.[1] While abandoned meadows lack some of the complexity and characteristics of active meadows, similar process may still occur in meadows of both activity levels. This is because historic beaver activity leaves an impact on a meadow that gradually degrades over time.[10] For example, Moraine Park, one of the abandoned meadows in this study, was noted in a 2012 study to be a site where beaver activity had greatly influenced post-glacial floodplain aggradation, despite having no beaver activity at the time of that study.[10]

The increased outflow abundance of the collector-filterer family Simuliidae and the collector-gatherer family Leptophlebiidae could suggest differences in availability of FPOM between meadow inflows and outflows. Simuliidae and other collector-filterers feed by capturing decomposing FPOM that is suspended in the water column as it travels downstream. Collector-gatherers such as Leptophlebiidae also feed on FPOM that has settled on the stream bottom.[8] One possible mechanism for patterns of increased collector-filterers and collector-gatherers at the outflows is that river-floodplain meadows add FPOM to the water as it travels through meadows. This would lead to increased levels of FPOM at outflows, creating a more favorable habitat for the Simuliidae and Leptophlebiidae. Floodplain meadows are known to trap particulate organic matter during flood events when the stream is forced out of the channel and into unconfined meadow segments.[1] However, the sampling for this study was performed in August, after all sites had passed their peak flows and flood events. Another possible mechanism for increasing FPOM at outflows is the gradual breakdown of woody debris stored within floodplain meadows, continuously creating particulate organic matter.[1] It is possible that the slow breakdown of woody debris in these meadows could be providing an abundant food source for collector-gatherers and collector-filterers at the meadow outflows.

While collector-filterers and collector-gatherers were more abundant at meadow outflows, the scraper mayfly family Heptageniidae, was found in greater numbers at meadow inflows. Since scrapers feed by grazing on periphyton attached to substrate, a difference in the amount of periphyton between inflows and outflows could be affecting the abundance of scrapers.[8] Nutrients stored near the sediment water interface promote patches of periphyton, which are also influenced by stream geomorphology and oxygen availability.[11] Scrapers are also specialist feeders, which makes them more sensitive to disturbances or pollutants that impact a specific food source, unlike collector-filterers, which are more generalist feeders.[9] Without further study, it is difficult to say which of many possible factors could be leading to lower Heptageniidae abundances at the meadow outflows.

Although technically statistically significant, results regarding differences between the inflow versus the outflow abundance of Dolichopodidae might not indicate anything about the impacts of land use and beavers. This family was only present in one location on one meadow, Mill Creek's inflow. It is possible that unique characteristics of Mill Creek's inflow are creating a favorable habitat for this family; these characteristics may or may not be related to the past land use and beaver activity in the downstream meadow.

Differences between active and abandoned meadows

Many aquatic insect taxa, including seven families and three entire orders, had higher abundance in active meadows compared to abandoned meadows, regardless of the location on the meadow. The families in **Figures 8 and 9** demonstrate examples of this type of relationship. Since inflows are assumed to be unaffected by the downstream meadow processes, one would expect to find differences between activity levels only when considering the outflows as they compare to inflows. However, since this is not the case, it appears that there are differences between active and abandoned meadows that are impacting stream communities at both inflow and outflow locations. There are several possible explanations for the overall increased abundances of certain taxa in active meadows.

For most of the aquatic insect taxa in this study, the adult forms are capable of flight. Adult aquatic insects are known to fly upstream from their larval habitat to lay eggs, resulting in upstream larval populations being supplemented by downstream populations.[12] If active meadow processes are creating particularly productive habitats at outflows, it is possible that some of the adults emerging from outflow habitats are traveling upstream to the inflow locations to lay their eggs. Active meadow outflows may be a highly productive habitat due to the downstream flux of nutrients from processes such as the breakdown of woody debris and frequent flood events occurring within active beaver meadows.[1,2]

A second possibility regards the idea that the presence or absence of beavers in these meadows is due in part to the meadow's land use history. Past land use could be influencing other overall characteristics of the streams and their riparian areas in addition to influencing whether the meadows are active or abandoned. An area's history could also be impacting the availability of food sources necessary for the presence of dietary specialists including scrapers such as Ameletidae, and shredders such as Nemouridae.[9]

While many families and orders were more abundant in active meadows, only two families were more abundant in abandoned meadows, Hydroptilidae and Hydropsychidae. Hydroptilidae are piercers that extract the contents of algae cells with specialized mouthparts.8 Algae may be more abundant in abandoned meadows than active meadows. When visiting these sites, it was observed that abandoned meadows sometimes had less riparian vegetation than active meadows. Less vegetation at abandoned meadows may be allowing more sunlight to penetrate the water and promote the growth of algae in abandoned meadows. Returning to sites and simultaneously sampling for algae and macroinvertebrates could help test this hypothesis. Meanwhile, Hydropsychidae are collector-filterers that construct a silk capture net which they use to strain out particulate matter. They are limited to particulate matter in a specific size range such that it won't pass through or break their capture net. It's possible that the streams with active meadows do not produce the correct size of particles for Hydropsychidae.

Interactions between meadow activity level and location

In this study, inflows of meadows of both activity levels were assumed to be equally unaffected by the processes occurring downstream in the meadow. When processes such as storage of woody debris and cycling of nutrients are unequal between active and abandoned meadows, there may be an interaction between meadow activity level and meadow location such that the relationship between inflow and outflow communities differs between active and abandoned meadows. The families in **Figures 10 and 11** demonstrate examples of this type of relationship.

One such interaction was observed in the scraper family Glossosomatidae, which was more abundant at outflows than inflows in active meadows, but not in abandoned meadows. This suggests that processes occurring in active meadows are leading to more favorable outflow habitats for Glossosomatidae or for their food source, periphyton. One possibility is that increased periphyton thrive downstream of active meadows due to increased nutrients stored in the sediments of active meadows.[11] Nutrient rich sediments stored both in and just downstream of active meadows could be due to higher carbon accumulation and retention in beaver meadows through processes such as flooding.1 It is also possible that competition for periphyton with other scraper taxa such as Heptageniidae affects the distribution and abundance of Glossosomatidae.

The collector-gatherer family Leptophlebiidae displayed the same interaction behavior as seen in the family Glossosomatidae. Collector-gatherers are one of the more generalist feeding groups of macroinvetebrates.[9] They eat decaying particulate matter trapped in the sediments.[8] Since active meadows are effective at trapping nutrients and particulate organic carbons in sediments during flood events, they may be contributing to downstream habitats with more nutrient-rich sediments, which would be a possible mechanism for the interaction behavior seen for Leptophlebiidae abundance.[1]

Although not statistically significant, it is important to note that other taxa displayed a similar interaction behavior to Glossosomatidae and Leptophlebiidae. Two examples are the shredder family Nemouridae and the collector-gatherer family Elmidae. Similar to Glossosomatide and Leptophlebiidae, both Nemouridae and Elmidae increased in abundance between inflow and outflow of active but not abandoned meadows. Shredders, such as Nemouridae, consume decomposing plant matter and wood, also called coarse particulate organic matter (CPOM).[8] The gradual breakdown of stored woody debris in active beaver meadows could result in more CPOM at outflows. Also, shredders, like scrapers, are a feeding group of dietary specialists, which makes them more sensitive to disturbances and pollutants that could impact their food source than other feeding groups.[9] Collector-gatherers like Elmidae are generalists that eat decomposing particulate organic matter trapped in substrates, which could be effected by meadow processes such as the trapping of nutrients. These insignificant interactions in Nemouridae and Elmidae could be due to a variety of differences between active and abandoned meadow processes or due to chance. Completing a similar study with more meadows and more replicates could be one way to investigate if there are interactions between meadow activity level and location in groups other than Glossosomatidae.

Dolichopodidae, Uenoidae, and Perlidae all displayed interactions as well. The interactions displayed by these three families involved a decrease in abundance between the inflow and outflow of the active meadow, and no change between inflow and outflow of the abandoned meadow. However, for Dolichopodidae, all six specimens found during this study were found at the inflow of Mill Creek, an active meadow. It is possible that characteristics unique to Mill Creek's inflow are creating a favorable habitat for this family; these characteristics may or may not be related to the past land use and beaver activity in the downstream meadow. Similarly, only three Uenoidae were found in this study and only in two places: the inflow of Mill Creek and the outflow of Hidden Valley. Again, since this family was only found in these two locations, it becomes increasingly questionable whether or not these patterns are related to river-floodplain meadow processes. Creating a statistical model that accounts for site-specific characteristics of the sampling locations could help determine if patterns in these rarely found families are significant to the processes of river-floodplain meadows. Perlidae, a predacious stonefly, displayed the same interaction as Dolichopodidae and Uenoidae, but was not as uncommon and was found repeatedly and at multiple locations. This predator may rely on some prey source that is more abundant at active inflows.

Conclusions and future actions

The use of aquatic macroinvertebrates as indicators of how anthropogenic disturbance affects stream quality has been repeatedly demonstrated by past studies.[3] While the specific mechanisms impacting the abundances of different taxa in these meadows is uncertain, it is clear that these meadows do affect the aquatic insect communities. The results of this study suggest that both active and abandoned meadows are affecting the outflow communities, and that in some cases the processes in active meadows benefit certain outflow taxa more strongly. Also it appears that some characteristic of the active meadows or their surroundings is resulting in increased abundance of several taxa both upstream and downstream of the active meadows. The use of aquatic insects as a biological indicator in this study supports the findings of past studies, which have shown that important ecological processes happen in both active and abandoned beaver meadows.[2,10] Both active and abandoned beaver meadows are ecologically significant areas and merit further study due to their importance to water quality and carbon cycling. Future studies could help link the macroinvertebrate community composition to the specific physiochemical and habitat characteristics of active and abandoned meadows. Since aquatic insects are effective biological indicators, processes impacting them could be causing much greater impacts on the stream ecosystem and downstream water quality.

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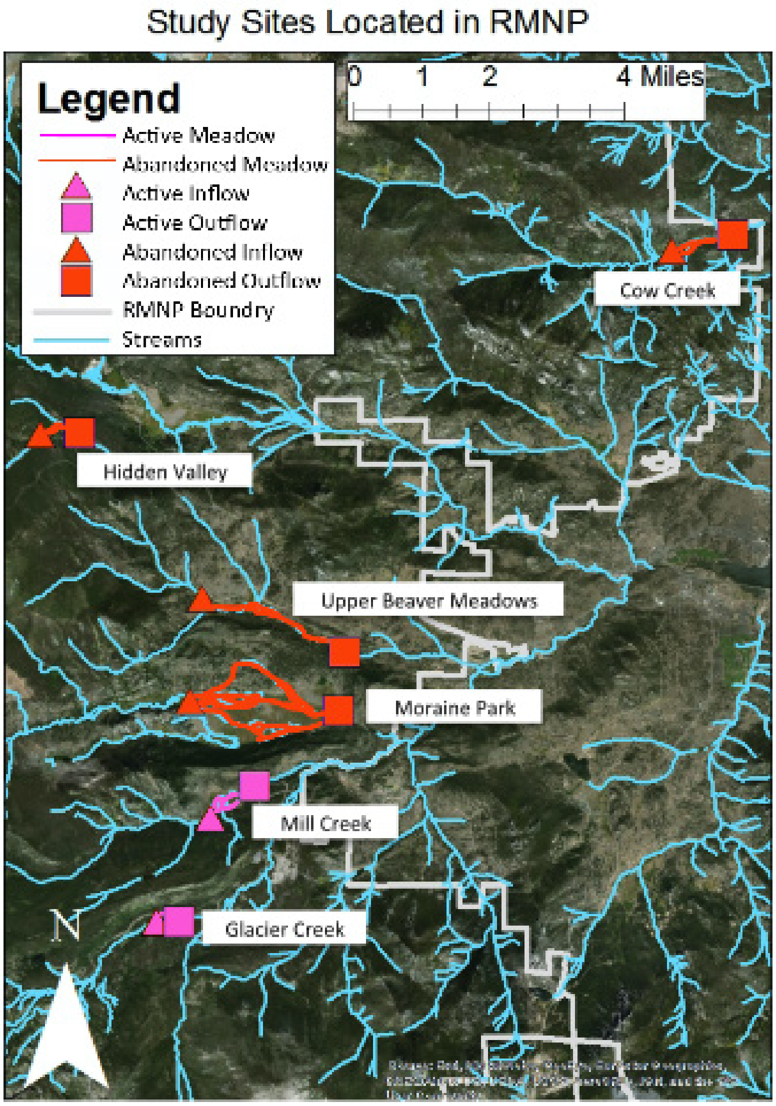


Figure 1: Study sites located in RMNP (left). Shows the 12 sampling locations at the inflows and outflows of the six river-floodplain meadows sampled for this study. All meadows are within the boundaries of Rocky Mountain National Park.

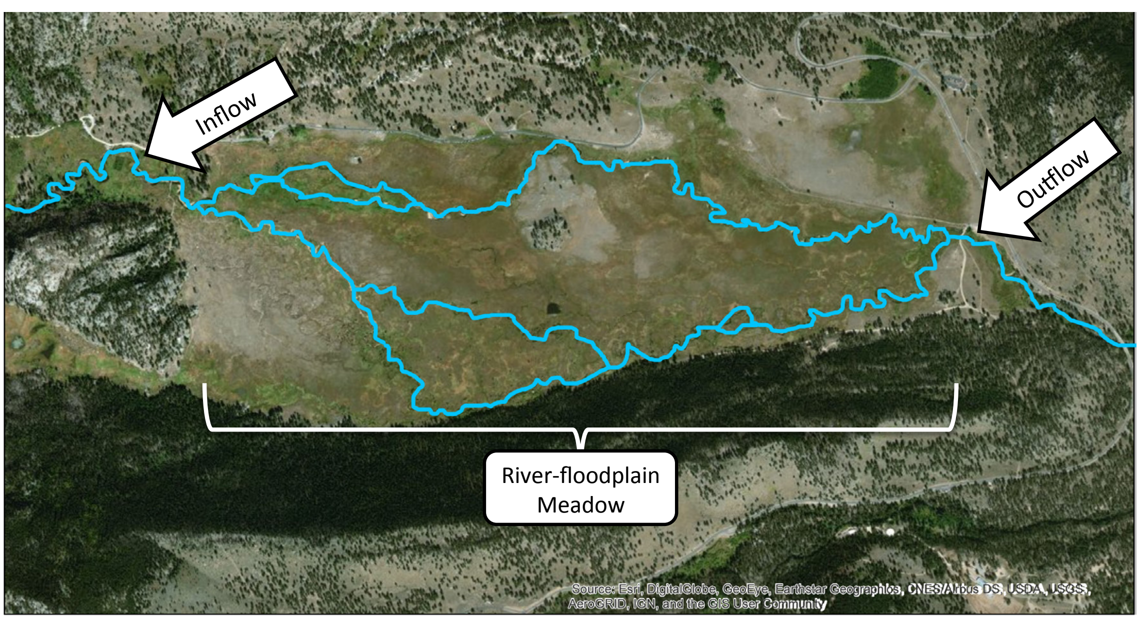


Figure 2: Meadow layout. A satellite view of Moraine Park, a river-floodplain meadow abandoned by beavers. The inflow and outflow sites are just above and below the section of stream that becomes braided as it travels across the meadow.

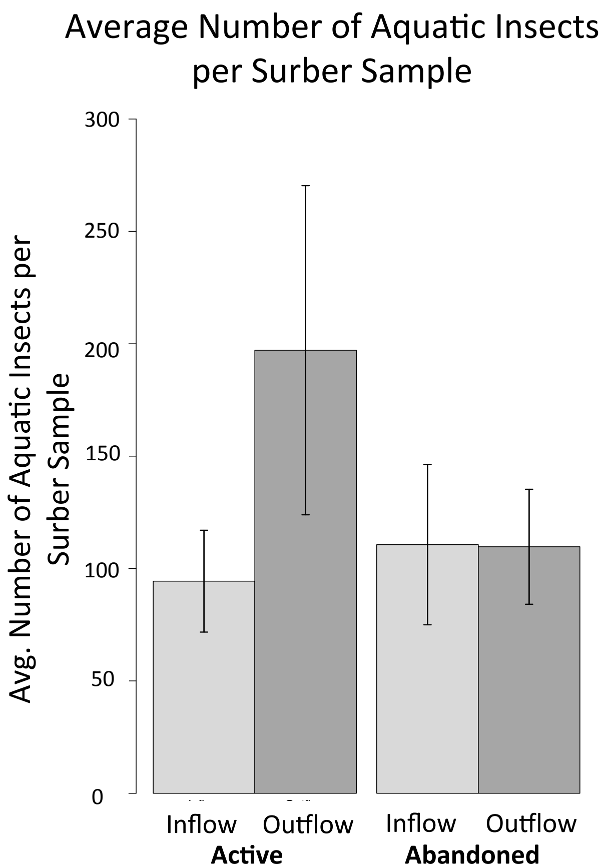


Figure 3: Average number of aquatic insects per Surber sample. This graph shows the average number of aquatic insects per Surber sample for each of the four treatment types: active inflow, active outflow, abandoned inflow, and abandoned outflow.

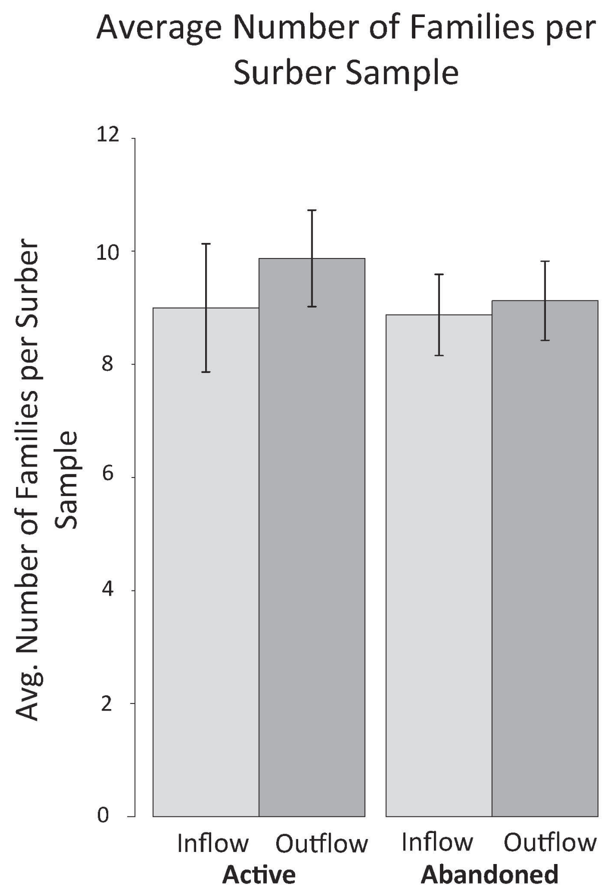


Figure 4: Average number of families per Surber sample. This graph shows the average number of different aquatic insect families per Surber sample found at each of the four treatment types.

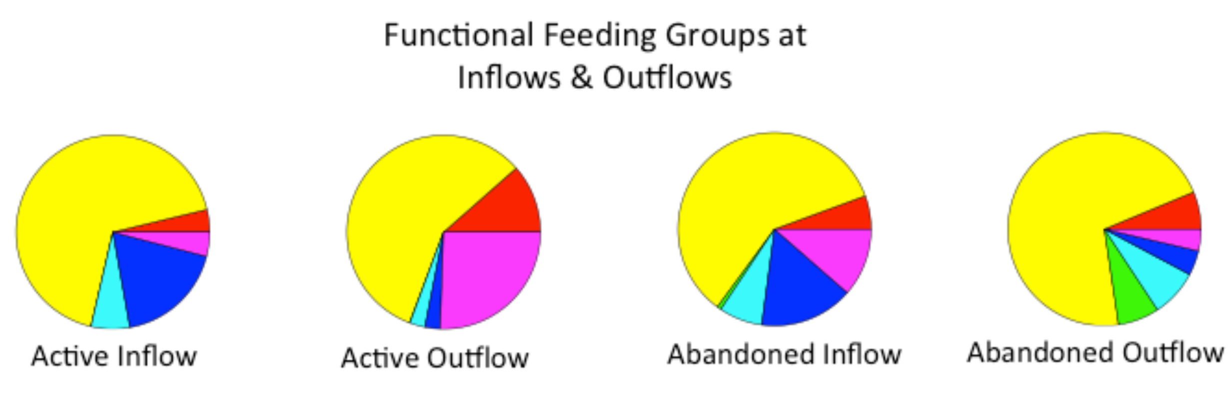
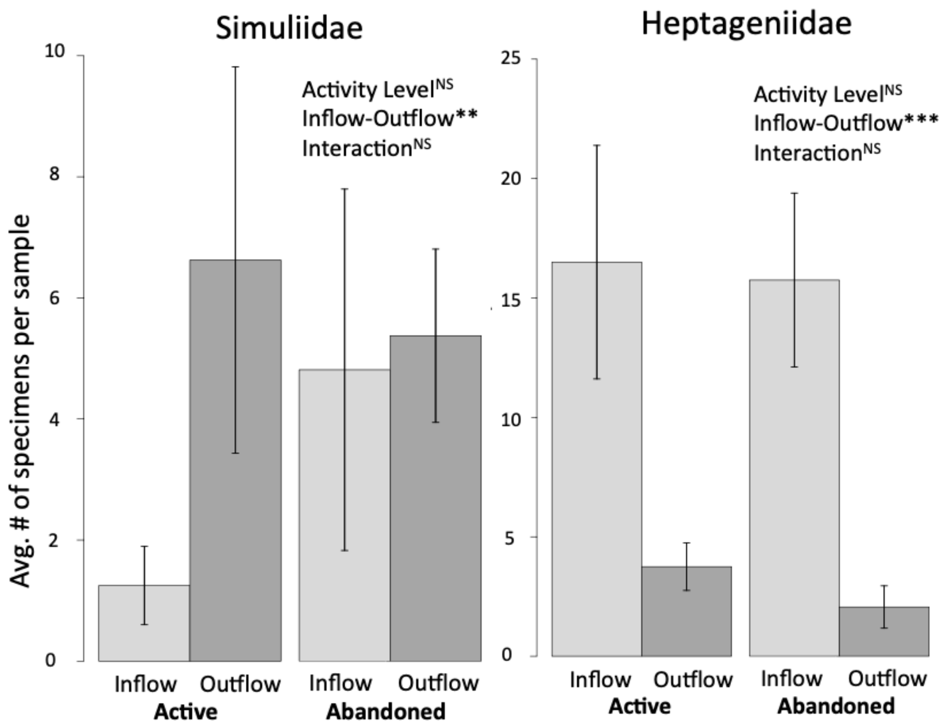
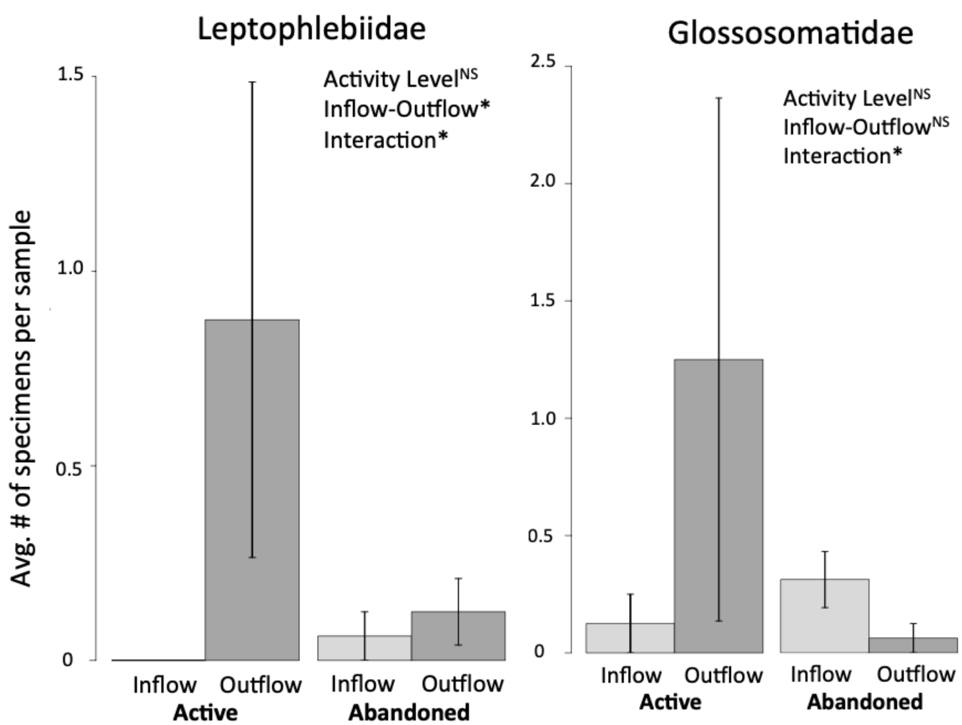


Figure 5: Functional feeding groups at inflows and outflows. Pie chart shows the relative abundances of the six functional feeding groups at the four different treatment types.



Figures 6 and 7: Examples of families that are significantly different between inflow and outflow locations. Figure 6 shows the average number of Simuliidae, a collector-filterer dipteran, which are more abundant at outflows than inflows. Figure 7 shows the average number of Heptageniidae, a scraper mayfly, which are more abundant at inflows than outflows.
*Significance codes for p-values: NS > 0.1; 0.1 > * > 0.05; 0.05 > ** > 0.01; *** <0.01*



Figures 10 and 11: Examples of families that demonstrate an interaction effect between activity level and location. Figure 10 shows the average number of Leptophlebiidae, a collector-gatherer mayfly, at the four treatment types. Figure 11 shows the average number of Glossosomatidae, a scraper caddisfly, at the four treatment types. Both Leptophlebiidae and Glossosomatidae demonstrate an intraction effect, with their greatest abundance occuring at active meadow outflows.

Research Process						
Project design and field site selection	→	Sample collection during field work	→	Taxonomic sorting of samples	→	Statistical analysis and data interpretation

Table 1: Conceptual diagram of the research process. This diagram outlines the steps taken in completing this study.

Meadow Name	Sampling Locations:	Active or Abandoned?
Cow Creek	Inflow	Abandoned
	Outflow	
Hidden Valley	Inflow	Abandoned
	Outflow	
Upper Beaver Meadows	Inflow	Abandoned
	Outflow	
Moraine Park	Inflow	Abandoned
	Outflow	
Mill Creek	Inflow	Active
	Outflow	
Glacier Creek	Inflow	Active
	Outflow	

Table 2: Site Classification. There were twelve total sampling locations on six meadows. Each meadow was sampled twice, once at the inflow and once at the outflow. All meadows are classified as either Active beaver meadows or Abandoned beaver meadows.

Order	Family	Feeding Habit	Significantly differed in abundance across:		
			Activity Levels	Locations	Interaction: Activity x Location
Ephemeroptera					
	Ameletidae	Scraper	Active**		
	Baetidae	Collector-gatherer	Active**		
	Heptageniidae	Scraper		Inflow***	
	Leptophlebiidae	Collector-gatherer		Outflow *	Active outflow *
Plecoptera					
	Chloroperlidae	Predator	Active**		
	Nemouridae	Shredder	Active *		
	Perlidae	Predator			Active inflow**
Trichoptera					
	Brachycentridae	Collector-filterer	Active***		
	Glossosomatidae	Scraper			Active outflow*
	Hydropsychidae	Collector-filterer	Abandoned *		
	Hydroptilidae	Piercer	Abandoned *		
	Uenoidae	Scraper			Active inflow**
Coleoptera					
	Elmidae	Collector-gatherer	Active***		
Diptera					
	Dolichopodidae	Predator	Active**	Inflow*	Active inflow **
	Simuliidae	Collector-filterer		Outflow**	

Table 3: Results by family. The table shows the functional feeding groups of aquatic insect families from this study. The last three columns indicate if the family was found to be significantly more abundant in active or abandoned meadows, inflows or outflows, and if there was any interaction effect between the two factors.
*1. Significance codes for p-values: NS > 0.1; 0.1 > * > 0.05; 0.05 > ** > 0.01; *** <0.01*
2. Families with only one total specimen found across all sites during this study were omitted from this list (Siphlonuridae, Dytiscidae, Dixidae, Ptychopteridae).
3. Families without significant ANOVA results were omitted from this list (Ephemerellidae, Perlodidae, Lepidostomatidae, Limnephlidae, Rhyacophilidae, Athericidae, Ceratopogonidae, Chironomidae, Emphidadae, and Tipulidae).

Order	Family	Abandoned Meadows								Active Meadows			
		Cow Creek		U.B. Meadows		Hidden Valley		Moraine Park		Mill Creek		Glacier Creek	
		Inflow	Outflow	Inflow	Outflow	Inflow	Outflow	Inflow	Outflow	Inflow	Outflow	Inflow	Outflow
Ephemeroptera		**16**	**14.5**	**18.25**	**40**	**63.75**	**22.75**	**39.25**	**25.75**	**47**	**67.75**	**31.75**	**31**
	Ameletidae	0.75	-	-	-	3	9.25	-	-	-	-	-	-
	Baetidae	5	7.75	3.25	36.5	35	5.25	6.25	12.75	11.5	45.75	22.5	23.5
	Ephemerellidae	6.5	6	5.5	2.75	4.25	7.75	4.5	6.25	11	17.25	0.75	2.75
	Heptageniidae	3.5	0.75	9.5	0.25	21.5	0.5	28.5	6.75	24.5	3	8.5	4.5
	Leptophlebiidae	0.25	-	-	0.5	-	-	-	-	-	1.75	-	-
	Siphlonuridae	-	-	-	-	-	-	-	-	-	-	-	0.25
Plecoptera		**3.25**	**12**	**2.75**	**19.75**	**49.75**	**9.5**	**2.5**	**0.5**	**11.5**	**104.25**	**4.5**	**4.25**
	Chloroperlidae	1.75	6	1.75	0.75	1.25	0.75	1	0.25	1.25	3	4.25	3.25
	Nemouridae	1.25	2.5	0.5	0.25	46	8.5	0.75	0.25	7.5	99.25	-	0.75
	Perlidae	-	2.25	-	-	-	-	-	-	1.5	-	0.25	0.25
	Perlodidae	0.25	1.25	0.5	18.75	2.5	0.25	0.75	-	1.25	2	-	-
Trichoptera		**8.5**	**35**	**1**	**3.25**	**13.5**	**1.75**	**2**	**1.75**	**5.75**	**32.25**	**1.25**	**3.25**
	Brachycentridae	1	2.25	-	-	-	-	0.5	1	3.5	31.25	1	0.25
	Glossosomatidae	0.25	0.25	-	-	-	-	1	-	-	-	0.25	2.5
	Hydropsychidae	3.5	2.5	-	-	-	-	-	-	-	-	-	0.25
	Hydroptilidae	3	29.5	-	0.25	-	-	-	0.25	-	-	-	0.25
	Lepidostomatidae	-	0.25	0.5	1.75	-	-	-	-	-	-	-	-
	Limnephilidae	-	-	-	0.75	0.5	0.75	-	-	-	-	-	-
	Rhyacophilidae	0.75	0.25	0.5	0.5	13	0.75	0.5	0.5	1.75	1	-	-
	Uenoidae	-	-	-	-	-	0.25	-	-	0.5	-	-	-
Coleoptera		**6**	**6**	**9.5**	**1**	**1.25**	**2**	**4.5**	**10**	**18.5**	**57.75**	**4.25**	**5**
	Elmidae	6	6	9.5	0.75	1.25	2	4.5	10	18.5	57.75	4.25	5
	Dytiscidae	-	-	-	0.25	-	-	-	-	-	-	-	-
Diptera		**76.75**	**138.5**	**1.25**	**13.25**	**81**	**60.75**	**32.5**	**16**	**44.75**	**79.75**	**16.75**	**6.25**
	Athericidae	0.25	-	-	-	-	1.25	-	-	-	0.5	-	-
	Ceratopogonidae	-	-	-	0.25	-	0.5	-	-	0.25	-	-	-
	Chironomidae	75.25	131.5	0.5	5	57	53.75	32.25	14	41	66.5	16.25	5.5
	Empididae	-	-	-	-	6.75	-	-	-	-	-	-	-
	Dixidae	-	-	-	-	0.25	-	-	-	-	-	-	-
	Dolichopodidae	-	-	-	-	-	-	-	-	1.5	-	-	-
	Ptychopteridae	-	-	-	-	-	-	-	-	-	0.25	-	-
	Simuliidae	1.25	6.5	0.75	7.75	17	5.25	0.25	2	2	12.5	0.5	0.75
	Tipulidae	-	0.5	-	0.25	-	-	-	-	-	-	-	-

Table 4: Averaged raw data. The table shows the raw averaged data, sorted by family. The abundance of each family is reported for each of the 12 sampling locations. Abundances reported here are the averages of 4 Surber samples taken per location. There were a total of 48 Surber samples taken during this study.