

Effects of single and terraced beaver ponds on benthic
macroinvertebrate communities

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ABSTRACT

Beavers are an important aspect of the landscape and have been increasing in abundance in montane regions of the western U.S. While beaver impoundments have been shown to affect downstream habitats, their influence is variable and may be attributed in part to variation in the morphology of impoundments. The purpose of this study was to estimate the effects of terraced and single beaver ponds on benthic macroinvertebrate functional feeding group composition and to test some potential mechanisms explaining differences between the two types of ponds. I took 30-s traveling kick samples of invertebrates and measured water chemistry, periphyton chlorophyll, seston AFDM, seston chlorophyll, and substrate particle size composition and installed Hobo continuous temperature and light recorders upstream and downstream of 6 beaver pond complexes (3 single and 3 terraced) in 2 montane catchments of the upper Gunnison River basin in western Colorado during summer 2007. Grazing invertebrates decreased in abundance downstream of single ponds, but increased downstream of terraced ponds, while suspension feeding invertebrates increased downstream of terraced ponds. There were too few shredders in these systems to test the effects of pond morphology on their abundance. Potential mechanisms for effects included increased ambient conductivity associated with higher grazer abundances, which could have caused higher primary productivity. Neither ammonium levels nor AFDM of seston explained abundance differences of grazers or suspension feeders upstream or downstream of impoundments. Water temperatures, phosphorus levels and chlorophyll in the periphyton and seston remain as viable hypotheses that will be tested when the data are completely analyzed. This study shows that beaver pond morphology should be taken into account when studying effects on stream ecosystems.

KEYWORDS: benthic, macroinvertebrate, invertebrate, beaver pond, impoundment, pond morphology

INTRODUCTION

The capability of North American beavers (*Castor canadensis*) to alter their environment through the cutting of timber and the creation of wetlands is truly remarkable and the effects are far reaching (Naiman, et al., 1986; Naiman, et al., 1988; Naiman, et al., 1994). Beaver dams, often built in terraced groups, raise the surrounding water table and visibly affect downstream habitats. However, some impacts of beaver modifications on stream hydrology are less obvious. Levels of key organic nutrients such as nitrogen and phosphorus can increase, decrease or remain unaffected in downstream aquatic habitats as a result of passage of water through beaver-altered systems (Maret, et al., 1987; Seitzinger, 1988; Margolis, et al., 2001). These conflicting results beg the questions: Why do effects appear to vary from pond to pond? What causes one beaver pond to affect downstream hydrology and biogeochemistry differently than another? The answers to those questions may be linked to variation in beaver pond morphology. In this study, I explore the relationship between pond morphology and functional feeding group composition of benthic macroinvertebrates, as well as some of the potential physical and biogeochemical mechanisms that generate that relationship.

In general beaver ponds reduce stream velocity (Parker, 1985). However, dams of varying dimensions create ponds of various shapes and sizes. Additionally, beaver ponds often occur adjacent to one another so that the effects of individual ponds are difficult to separate from

those of their neighbors. Differences in water flow over and around dams and through groundwater pathways are likely to affect both water temperature and nutrient content of downstream reaches through increased retention times and mixing with colder and more nutrient-rich groundwater. Such variations may result in different beaver ponds having different effects on local hydrology and nutrient availability to aquatic producers and consumers. Consequently, by affecting the physicochemical state of streams, beaver ponds also affect food availability for benthic invertebrate communities.

Benthic invertebrates can be divided into several functional feeding groups. These groups include *grazers* which feed on periphyton, *shredders* which feed on coarse particulate organic matter (CPOM), *suspension feeders* which feed on fine particulate organic matter (FPOM) and *predators* which feed on other invertebrates (Cummins, et al., 1979). Beaver ponds can filter suspended solids from streams as well as alter dissolved nutrient composition and water temperature downstream, both of which are conditions that affect algal growth (Maret, et al., 1987). Downstream of a beaver pond, the availability of algae and suspended organic material, or detritus, is likely to be influenced by the morphology of the associated dam and pond. As a result of influencing food resources, pond morphology has the potential to influence benthic macroinvertebrate communities which are largely defined by the availability of those food resources. In contrast to reaches downstream of beaver impoundment sites, the hydrology, chemistry and biology of the stream reach upstream of a beaver pond may function independently of pond morphology.

In general, one would expect that, during the day, water temperature would increase as water velocity decreases: when water being heated by the sun is retained as it warms rather than allowing it to flow downstream unobstructed. Thus, if retention time increases as water passes through a beaver pond, it is likely that water temperature downstream of the pond would increase. However, if high hydraulic head forces water in deep beaver ponds to downwell and then upwell downstream after mixing with groundwater, the areas of upwelling water would be colder and might contain higher nutrient levels. Furthermore, in a phosphorus-limited system such as many streams in the Upper East River drainage basin (Moslemi, *unpublished data*), any alterations to phosphorus availability would likely directly affect algal growth rates and also the abundance of algal *grazers*. Additionally, settling of particles and physical filtration of water passing through a pond and dam might lessen the amount of detritus entering the downstream reach, decreasing *shredder* abundance downstream of the dam.

By comparing functional feeding group composition and hydrological conditions within paired benthic communities from stream reaches upstream and downstream of beaver ponds, I investigated whether benthic communities downstream of beaver pond systems differ in composition due to beaver pond influence. Using the upstream reach as a reference site, differences between upstream and downstream reaches may be attributed to the pond system's effects on the stream.

Via effects on hydrology and biogeochemistry, beaver pond morphology could be important in determining invertebrate functional feeding group composition. By comparing benthic communities downstream from single and terraced beaver pond systems, I investigated the effects of pond terracing. Phosphorus is *adsorbed* (bound to clay particles) in oxic conditions and *desorbed* (becomes unbound from clay particles) in anoxic conditions (Christophoridis and Fytianos, 2006). Thus, the larger downward force on water in a deep pond is likely to cause an increase in water flow through anoxic conditions under the dam (White, 1990). Under anoxic conditions bound phosphorous will become *desorbed* and available via upwelling downstream of

a high dam. An influx of available phosphorus in the phosphorous-limited downstream reach would likely increase algal growth and *grazer* abundance.

With less downwelling, less water containing phosphorus will come in contact with anoxic groundwater, but will instead get “stuck” (remain adsorbed to clay particles) as it encounters oxic conditions in the dam (Christophoridis and Fytianos, 2006). Thus, terraced pond systems, comprised of a series of low dams, may act as phosphorus sinks, and the region downstream (which is already phosphorus-limited) might experience a decrease in available phosphorus. This decrease would likely be reflected in decreased algal growth and *grazer* abundance downstream compared to stream reaches upstream of the ponds.

A series of terraced ponds would have the potential to result in greater water warming than a single pond, though terraced ponds, when considered cumulatively, may represent a change in elevation similar to a deeper single pond. Additionally, the depth of water in each individual shallow pond comprising a terraced system would not likely be sufficient to create strong downwelling zones similar to those in deeper ponds. Thus, water flowing through terraced ponds might not experience a large amount of downwelling, and most water would enter the downstream reach via transport through the oxygen-rich conditions of the dam. Water passage through oxygenated dam substrate might allow the pond and dam to trap phosphorus, limiting algal growth and *grazer* abundance downstream of the shallow ponds which make up terraced systems. Benthic *suspension feeders*, known to colonize lake outlets, are likely to increase below both single and terraced beaver pond systems (Ciborowski, et. al., 1989). Finally, I predicted that shredder abundance would decrease below both types of pond systems, with a larger decrease occurring below terraced ponds. It is likely that CPOM will settle out of water as it passes through the slower-moving pond region, as well as being physically filtered by passage through or under a dam. An increasing number of ponds and dams to pass through, such as within a terraced pond system, might allow a larger proportion of CPOM to settle or filter out. Those decreases in available detritus downstream would likely be reflected by a decrease in *shredder* abundance downstream.

METHODS

Samples were taken of benthic invertebrate communities from upstream (reference sites) and downstream (modified sites) of six beaver impoundment sites. Each site was comprised of either a single or terraced beaver pond system, with both categories represented by three replicates. Each category was represented on both West Brush Creek and Coal Creek: two of each category on West Brush Creek and one of each category on Coal Creek. Surface areas and submeter global locations of each pond and sample site were determined using the GeoXT GPS system and are available on the rmbl.org website.

All invertebrate samples were taken on the 2nd-3rd of July 2007 using a traveling kick sample method (Gowns, et. al., 1997). All benthic samples were taken over a 30 second period using a D-net with approximately 1mm gauge mesh. Samples were taken across transects of the first riffle upstream and the first riffle downstream of each pond system. Two 30 second samples were taken from each stream reach by disturbing the substrate by hand. All *grazers*, *shredders* and *collectors* from the first 30 second sample were picked and identified to family in the field, then preserved in a solution of 90% ethanol for counting and further analysis in the laboratory. The second 30 second sample was inspected for rare taxa only.

Additionally, water samples were taken from each sample site on the 24th and 25th of July 2007 and analyzed for ammonium content using a fluorometer. Water samples also taken on the

25th of July 2007 were frozen and will later be analyzed for phosphorus content at the University of Wisconsin. Two liters of water were collected at each sample site and from the dam spillover of each system's lowest dam on August 1st-3rd. To obtain seston ash-free dry mass (AFDM), two L of water from each sample site were suction filtered, dried at 40-60°C for 48 hours, weighed, and combusted in a muffle furnace at 500°C for one hour to obtain a final mass (Hauer and Lamberti, 1996). Seston chlorophyll data from each two L spillover sample is forthcoming, and chl-*a* concentration will be determined using a fluorometer. Additionally, measurements of periphyton availability at each sample site are forthcoming.

HOBO temperature-light loggers were installed at each sample site to obtain a long-term picture of temperature patterns. Additionally, ambient and specific conductivities were measured at each sample site on the 31st of July 2007 and the 2nd and 3rd of August, 2007. Substrate particle size composition was characterized at each sample site using zigzag particle counts (Hauer and Lamberti, 1996). Stream reaches used for zigzag particle counts extended from the lowest dam of the pond system to 42m downstream of the lowest dam, and from the upstream boundary of visible pond influence to 42m upstream of visible pond influence. Visible pond influence was defined by backflow or stagnation of water flow.

Each of the parameters described above will be measured for both reference and modified sites as possible mechanisms explaining differences in invertebrate functional groups. Using a paired design, comparing samples from upstream/downstream of each site, beaver pond influences were compared between stream sites using two-tailed t-tests. I also tested for relationships between physical/chemical factors and the ratios of functional feeding group abundance downstream vs. upstream using Spearman Rank correlation analysis. The differences between substrate particle size composition between upstream and downstream reaches were tested using Kolmogorov-Smirnov two-sample tests.

RESULTS

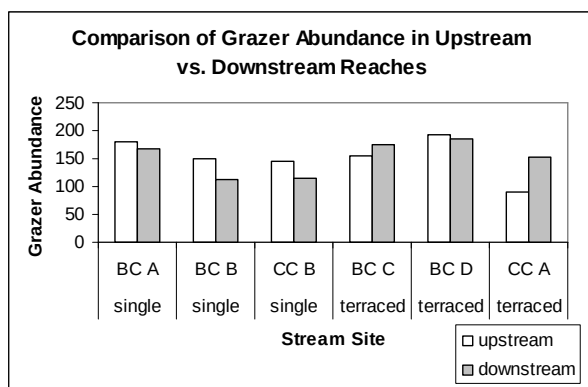


Figure 1—Numbers of grazing invertebrates collected upstream (clear bars) and downstream (gray bars) of single and terraced beaver dams in 30 second traveling kick samples. CC=Coal Creek, BC=West Brush Creek, A,B,C and D designate relative positions on stream, with A representing most downstream pond system, B representing second most downstream pond system, etc.

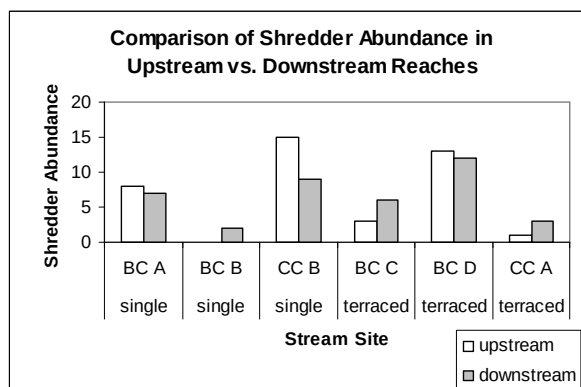


Figure 2 –Numbers of shredding invertebrates collected upstream (clear bars) and downstream (gray bars) of single and terraced beaver dams in 30 second traveling kick samples. Site name abbreviations as in Figure 1.

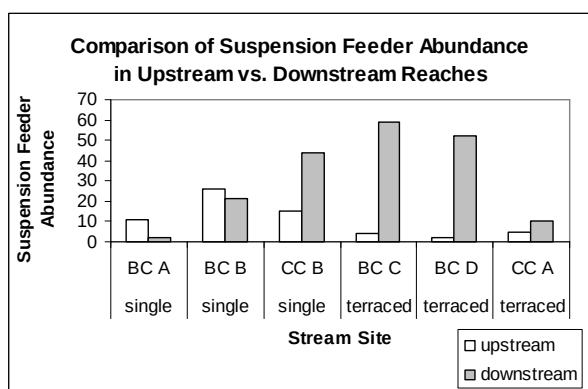


Figure 3—Numbers of suspension feeding invertebrates collected upstream (clear bars) and downstream (gray bars) of single and terraced beaver dams in 30 second traveling kick samples. Site name abbreviations as in Figure 1.

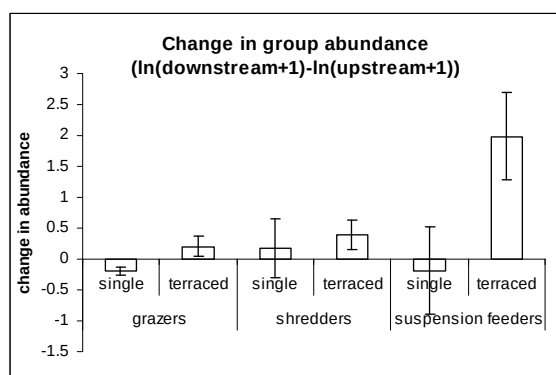


Figure 4—Changes in mean group abundances between reaches upstream and downstream of each pond type. Values were log transformed according to the formula: $\ln(\text{downstream}+1)-\ln(\text{upstream}+1)$

Grazing invertebrates were exclusively mayflies in these streams, primarily in the families Baetidae (*Baetis*) and Heptageniidae (e.g. *Epeorus* and *Cinygmula*). They exhibited a declining trend in mean abundance below single dams and an increasing trend in mean abundance below terraced dams (Figs. 1 and 4). A two-tailed t-test suggested that grazer abundance downstream of single and terraced ponds are affected differently by single and terraced pond systems ($df=4$, $t=-2.2278$, two-tailed $p=.08983$). There were only 79 shredders (mostly Nemouridae stoneflies) obtained in all samples (compared to 1821 grazers and 251 suspension feeders), which exhibited no pattern with respect to pond type (Figs. 2 and 4; $df=4$, $t=-.41935$, two-tailed $p=.696503$). Suspension feeders (Simuliidae and Hydropsychidae) exhibited increasing mean abundance below terraced dams, and variable mean abundance below

single dams (Figs. 1 and 4; $df=4$), and a two-tailed t-test also suggested that the effects of terraced and single dams differed ($t=-2.19774$, two-tailed $p=0.092886$).

site	pond type	ammonium upstream (ug/L)	ammonium downstream (ug/L)	ammonium change (downstream-upstream ug/L)
Brush Creek A	single	1.07425	1.04617	-0.02808
Brush Creek B	single	2.46966	1.41208	-1.05758
Brush Creek C	terraced	1.72138	1.94481	0.22344
Brush Creek D	terraced	2.07165	2.72898	0.65733
Coal Creek A	terraced	2.21576	2.82072	0.60496
Coal Creek B	single	1.41390	2.52737	1.11346

Table 1—Dissolved ammonium levels for all sample sites and dissolved ammonium level differences between upstream and downstream reaches. Site name abbreviations as in Figure 1.

The change in dissolved ammonium between upstream and downstream reaches was not significantly different between single and terraced dams (Table 1, $df=4$, $t=-.75727$, $p=0.491046$). Additionally, there was no significant relationship between ammonium content and dam height ($R^2=.1148$).

Kolmogorov-Smirnov two-sample tests, showed that substrate particle size distributions were not significantly different between upstream and downstream reaches at any of the 6 sites.

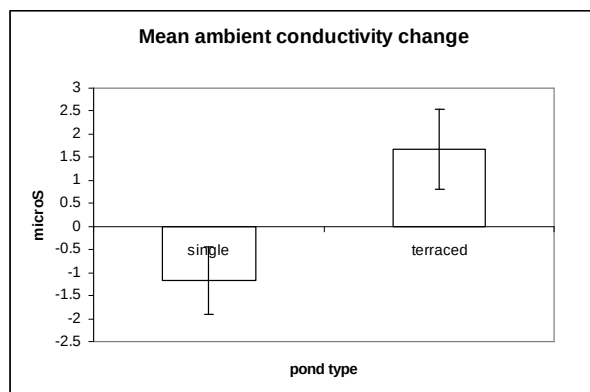


Figure 5—Mean ambient conductivity change between upstream and downstream reaches for single and terraced systems.
Conductivity change=downstream value-upstream value

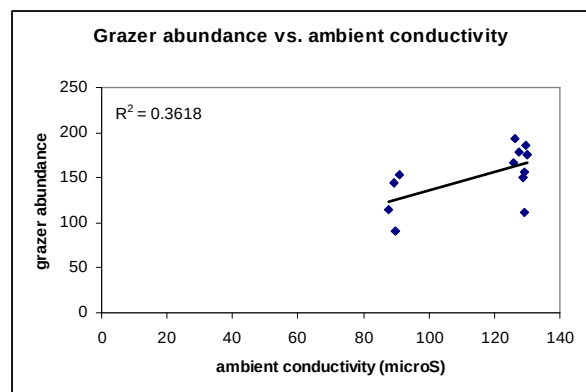


Figure 6—Grazer abundance for all twelve sample sites, correlated with ambient conductivity values for all twelve sample sites.

Mean ambient conductivity differed between single and terraced ponds (Fig. 5; $df=4$, $t=-2.48926$, two-tailed $p=0.067538$), but the effect sizes were very small. There was a weak correlation between ambient conductivity and grazer abundance, shown by Fig. 6 ($R^2=.3618$), and a Spearman's Rank Correlation showed a weak correlation between ambient conductivity and grazer abundance ($R_s= 0.48951$).

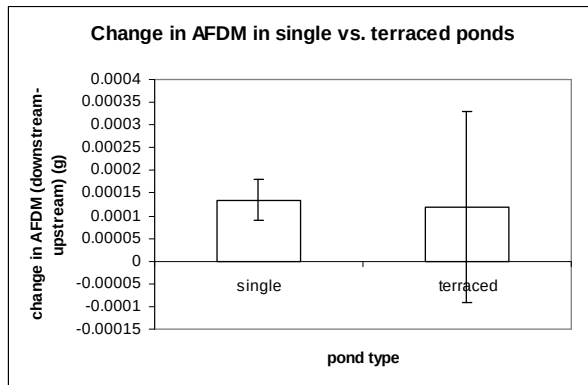


Figure 7—Change (downstream value-upstream value) in ash-free dry mass for single and terraced systems.

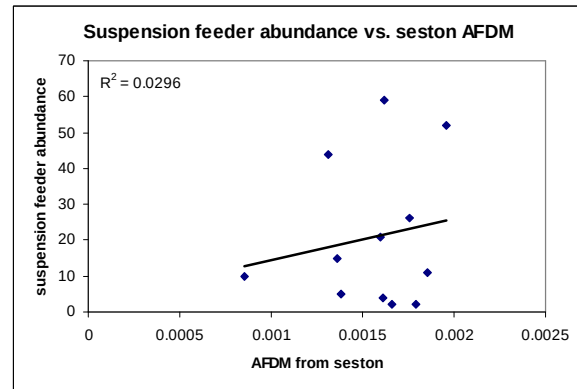


Figure 8—Suspension feeder abundance for each of twelve sample sites correlated with ash-free dry mass for each site.

Ash-free dry mass (AFDM) from seston increased in stream reaches downstream of single ponds and varies in stream reaches downstream of terraced systems, but did not differ significantly between the two systems (Fig.7; $df=4$, $t=.072628$, two-tailed $p=.945589$). Additionally, there was no correlation between AFDM and suspension feeder abundance (Fig. 8, $R^2=.0296$; $R_s=0.027972$).

DISCUSSION

Data collected thus far have shown intriguing trends in grazer and suspension feeder abundances in response to pond morphology. Grazers tended to decrease in abundance below single ponds and increase in abundance below terraced ponds (Figs. 1 and 4). Ambient conductivity showed a relationship with pond morphology similar to that of grazers (Fig. 5), decreasing below single ponds and increasing below terraced ponds. While effect sizes were small, differences in stream chemistry between ponds with different morphology are a possible explanations for functional feeding group effects. Conductivity readings from sample sites within each stream did not vary from each other by more than $4.2\mu S$, which could be attributed to instrument error. Additionally, there was only a weak correlation shown between ambient conductivity and grazer abundance ($R_s= 0.48951$). However, several other mechanisms can be ruled out as defining grazer abundance including ammonium levels and seston AFDM, neither of which is a likely cause for grazer or suspension feeder abundance differences between pond types. Substrate particle size also may be ruled out as a factor causing benthic community differences between upstream and downstream reaches for all sample sites.

Forthcoming data on long-term temperature, light, phosphorus levels and periphyton availability might shed some additional light on the question of which mechanisms play the largest roles in altering grazer abundances downstream of beaver ponds. Phosphorus, likely the limiting nutrient in Brush Creek and Coal Creek, as well as light and temperature, could have important effects on periphyton, which is the primary food source for grazers, and thus grazer populations themselves.

Shredder abundances were very low for all sample sites. Seventy-nine total shredders were collected from the 12 samples sites, for an average of less than 7 individuals represented at each sample site. With such low shredder abundances, these systems are not suitable to test the initial hypotheses set forth by this project concerning shredder abundances.

Suspension feeders demonstrated variable abundances below single ponds and consistently increased abundance below terraced systems (Figs. 3 and 4). AFDM of seston samples revealed that the mass of organic seston increased below single ponds and varied below terraced systems (Fig. 7). Thus, this variable does not explain suspension feeder abundance patterns (Fig. 8 $R^2=0.0296$; $R_s=0.027972$). However, AFDM of seston provides a measure of all organic material present, regardless of its quality as food. For selective feeders such as *hydropsychids* and *simuliids* (Wallace and Merritt, 1980; Shepard and Minshall, 1984), the primary suspension feeders present in the systems studied, a measure of food availability that takes quality into account may be necessary to understand the mechanisms defining changes in abundance. Forthcoming chlorophyll data from seston will provide additional information on food quality and availability for suspension feeders.

This data set enables preliminary narrowing of possible mechanisms that might explain the differences shown between benthic macroinvertebrate communities associated with beaver ponds of differing morphologies. However, the key observation that benthic communities differed as a result of their associations with differing beaver pond morphologies is an important consideration for all future studies that might otherwise consider all beaver ponds to have similar effects. This study indicates that such similarity is simply not the case, and when conducting research that concerns beaver pond effects, pond morphology must be taken into account.

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