Hydrobiologia (2011) 668:35–48
DOI 10.1007/s10750-011-0611-x

TRIBUTE TO STANLEY DODSON

# Does the morphology of beaver ponds alter downstream ecosystems?

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Received: 3 June 2010 / Accepted: 18 January 2011 / Published online: 2 February 2011
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**Abstract** Differences among lake morphologies often explain variation in characteristics of lentic ecosystems. Although beaver ponds also vary in morphology, previous studies have not examined the effects of such variation on downstream ecosystems. This study evaluated downstream effects of multiple beaver ponds in the Colorado Rocky Mountains during one low and one high-flow year. Beaver pond morphology was described as the natural log transformed ratio of beaver dam height (which determines hydraulic head) to pond surface area and related to pond spillover phytoplankton and characteristics of the ecosystem downstream (nutrient concentrations, limiting nutrients, periphyton, benthic organic matter (BOM), and benthic invertebrate consumers). Nitrate concentration increased systematically downstream of beaver ponds, but only in the low flow year when groundwater influences predominated. Effects of beaver ponds on soluble reactive phosphorus concentration depended on pond morphology, increasing downstream of small ponds with high dams, but only during the low-flow year. In situ experiments showed that neither beaver activity nor pond morphology predicted periphyton-limiting nutrients downstream. Both periphyton biomass and BOM decreased downstream of small ponds with high dams but pond morphology did not predict abundance of invertebrate grazers or detritus-feeding consumers. While suspension feeding invertebrates increased downstream from small ponds with high dams, variation in chlorophyll *a* from water spilling over beaver dams did not follow a similar pattern. We conclude that the effects of beaver ponds on downstream nutrients, resources and consumers are rarely systematic, but instead depend on variation in pond morphology and on annual hydrologic variation.

**Keywords** Beaver (*Castor canadensis* Kuhl) · Nutrients · Benthic algae · Macroinvertebrates · Benthic organic matter · Rocky mountain streams

Guest editors: H. J. Dumont, J. E. Havel, R. Gulati & P. Spaak / A Passion for Plankton: a tribute to the life of Stanley Dodson

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## Introduction

The ability of the North American beaver (*Castor canadensis* Kuhl) to alter its environment has been appreciated by hydrologists, geomorphologists and

ecologists for decades (Rosell et al., 2005). Beaver ponds were once ubiquitous across North American lotic systems and are currently returning to pre-European settlement densities (Naiman et al., 1988; Foster et al., 2002; Cunningham et al., 2006). Predicting the location of beaver ponds in watersheds has been approached from a beaver food-resource perspective (Dieter & Mccabe, 1989) as well as a geomorphology perspective (Jakes et al., 2007). Results from those studies suggest that beavers primarily inhabit streams where discharge is low enough for a dam to be stable and adequate food resources are available. The insertion of lentic pond habitats into smaller, lower order streams constitutes a major discontinuity of the system (Ward & Stanford, 1983). Therefore, considering the growing populations of beavers throughout temperate systems, understanding the influence of beaver-engineered structures embedded in otherwise continuous stream networks is vital for understanding the fundamentals of longitudinal stream processes (Jones et al., 1994, 1997).

In addition to the potential of beaver ponds to disrupt lotic stream habitats, there is also enormous variability among the lentic habitats created by beavers. Beaver ponds vary substantially in surface area and dam height, and those geomorphic differences among ponds could potentially have predictable impacts on nutrient dynamics and food webs of downstream reaches. For example, constructed wetlands of varying size and shape have dramatically different nitrogen and phosphorus processing as well as total suspended solids transport (Arheimer & Wittgren, 1994, 2002; Koskiaho, 2003; Reinhardt et al., 2005; Tonderski et al., 2005). Results from wetland systems provide a reasonable conceptual framework for predicting the effects of beaver ponds on downstream nutrient availability, algal resources, and benthic organic matter transport. While some studies have documented effects of beaver ponds on water chemistry (Devito & Dillon, 1993; Correll et al., 2000, Margolis et al., 2001b), periphyton (Coleman & Dahm, 1990), and sedimentation (Butler & Malanson, 1995), only site-specific mechanisms have been offered to explain the observed variation among downstream effects.

What distinguishes beaver ponds from other wetland systems is the dramatic change they cause in the hydrology of stream systems. Beaver-altered systems have a wide range of impacts on groundwater flow patterns (White, 1990; Westbrook et al., 2006). Additionally, streambed substrate hydraulic conductivity is altered downstream of beaver dams (Genereux et al., 2008) in favor of greater groundwater upwelling. Nutrients within these upwelling hyporheic and groundwater flows are then available to streambed biofilms (Coleman & Dahm, 1990). If varying beaver pond morphology results in different rates of upwelling downstream of the ponds, then nutrient availability should vary predictably downstream of beaver ponds.

Furthermore, if beaver ponds alter stream water nutrients and/or benthic organic matter transport in bottom-up controlled trophic systems, such alterations to basal resources may potentially affect consumers (Power, 1992; Wallace et al., 1997). Studies comparing benthic stream invertebrate assemblages upstream and downstream of beaver ponds (McDowell & Naiman, 1986; Smith et al., 1991; Clifford et al., 1993; Margolis et al., 2001a) often report inconsistent effects. For example, previous studies have reported higher densities of invertebrate suspension feeders downstream of beaver ponds (Clifford et al., 1993; Margolis et al., 2001a), no significant changes in suspension feeder abundance (McDowell & Naiman, 1986), or decreased abundance downstream (Smith et al., 1991). Comparative studies are needed to identify factors potentially explaining the variation among observed effects of beaver ponds on downstream ecosystems.

The goals of this study were to evaluate whether effects of beaver ponds on downstream ecosystems were systematic, or if variation in beaver pond morphology could explain the variation in effects of beaver activity on downstream ecosystems. We hypothesized that stream reaches below ponds with high-hydraulic head dams and small surface areas would have higher nutrient concentrations due to greater groundwater upwelling into the downstream reach. Additionally, we tested for relationships between pond morphology and downstream nutrient limitation, periphyton, benthic organic matter, and pond spillover phytoplankton as potential resources for invertebrate consumers. Finally, we tested effects of beaver ponds in general and pond morphology in specific on invertebrate consumers downstream.

## Materials and methods

### Study sites

Study sites were located near the Rocky Mountain Biological Laboratory on the western slope of the Colorado Rocky Mountains near Crested Butte, Colorado, USA. Twelve beaver ponds were studied during summer 2007 from 4 catchments (Coal Creek (2 ponds), East Brush Creek (3), Oh-Be-Joyful Creek (3) and West Brush Creek (4)), and 10 beaver ponds during summer 2008 from two catchments (Cement Creek (6) and West Brush Creek (4)) (Fig. 1). The West Brush Creek sites were studied in both 2007 and 2008. Each site consisted of a specific geomorphic pattern: an upstream lotic reach, lentic pond, and downstream lotic reach. This site design was chosen to isolate the effects of a single pond on the downstream reach by comparison to a reference reach directly upstream of the pond. All dams were on the main stem of the river and were either overflow or gapflow dams (Woo & Waddington, 1990). The annual hydrologic regimes in 2007 and 2008 were very different; in 2007 the snow cover and stream flows were low compared to the 15 year average, and the 2008 snow cover and stream flows were among the highest on record (also, see Fuller & Peckarsky, in press for more details about the study sites).

In this comparative study, beaver ponds were selected to maximize variation in sizes and shapes. A principle components analysis (PCA) evaluating

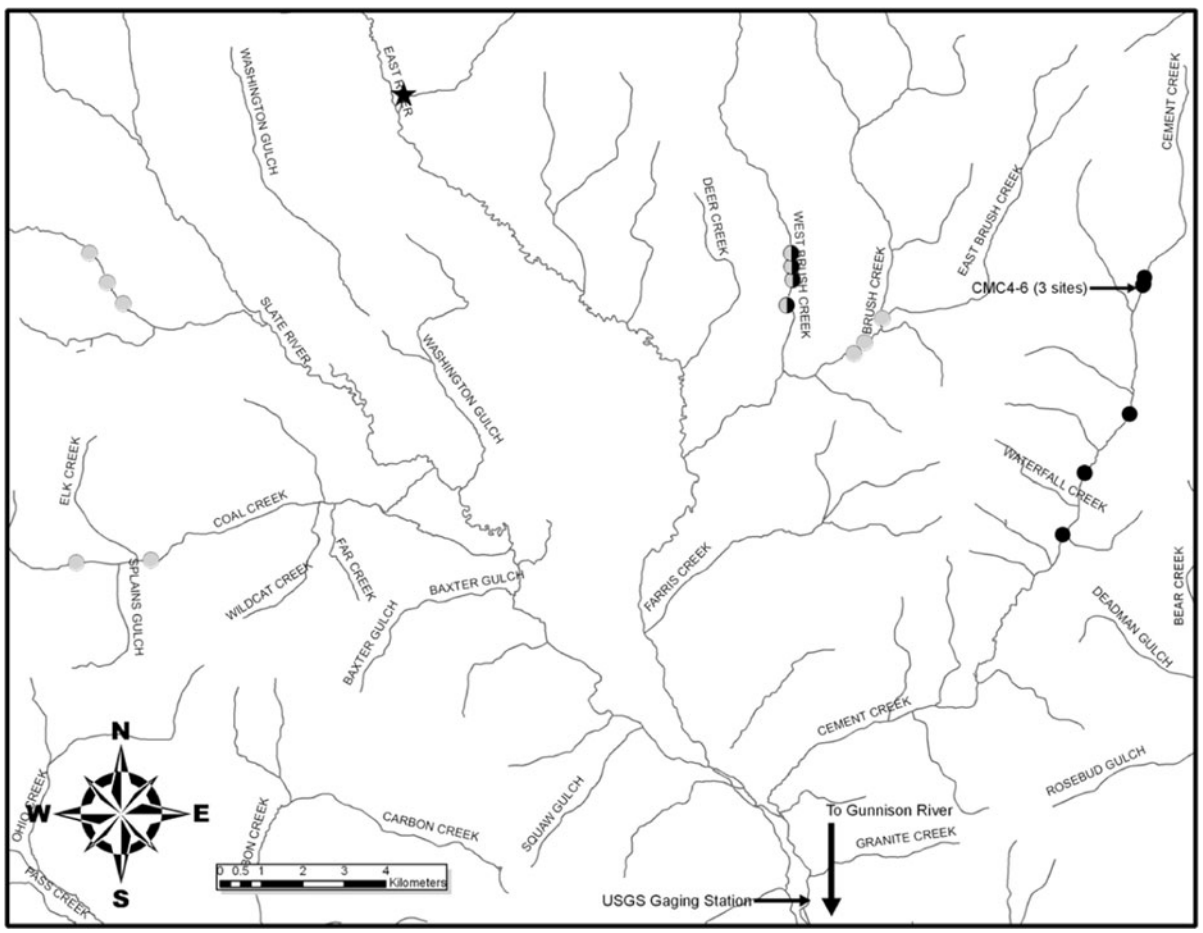


**Fig. 1** Map of study sites. Asterisk indicates the Rocky Mountain Biological Laboratory. *Gray circles* are sites sampled in 2007, *half black circles* are sites studied in both 2007 and 2008 and *black circles* are sites studied in 2008. The location of the USGS gauging station (09112200), which was the source of the data on annual hydrographs (reported in Fuller and Peckarsky, in press), is on the East River just downstream of the Cement Creek confluence

hydraulic height (or dam height), pond surface area, pond length, and maximum pond width was used to determine which pond dimensions explained the greatest variation among sites (Fuller & Peckarsky, in press). Hydraulic heights (measured as the distance from the water surface of pond to the water surface of the downstream reach) ranged from 0.28 to 1.77 m in 2007 and from 0.42 to 2.43 m in 2008. Surface areas of ponds ranged from 0.031 to 0.497 ha (2007) and 0.013 to 0.162 ha (2008). Pond lengths (linear distance from pond inlet to dam) were generally short, ranging from 20 to 90 m (2007) and 15 to 50 m (2008), supporting the assumption that natural longitudinal change within a stream would have been minimal in the absence of the beaver pond. Therefore, we attributed the observed differences between upstream and downstream reaches of a beaver pond to the presence of the pond. Based on the results of the PCA, ponds were arrayed along an axis of dam height/pond area ratios, with smaller ratios indicating low-head, large surface area ponds and higher ratios being high-head, small surface area ponds. Measurements of pond surface area and all linear distances were made using a Thales ProMark3 GPS unit with an $x$–$y$ plane accuracy of $\pm 1$ cm, and data were analyzed using ArcMap 9.2 (ESRI, 2009). Vertical measurements of dam heights were made using a surveying autolevel with an accuracy of $\pm 1$ cm.

## Stream water nutrient concentrations

Stream water samples were collected once each summer from 24 to 29 July 2007 and 4 to 5 August 2008 to compare nutrient concentrations upstream and downstream of each pond as well as the pond spillover. Samples were taken approximately 3 weeks after baseflow conditions had been achieved in 2007, but during the tail of the descending limb of the annual hydrograph in 2008 because of high water and late snowmelt conditions that year. Samples were filtered in the field using a 60 ml syringe and filter housing (0.7 μm pore size Whatman glass microfiber filter). Soluble reactive phosphorus (SRP), nitrate–N ($NO_3$–N) and ammonium–N ($NH_4$–N) samples were frozen for later analysis. Samples were analyzed on an Astoria Pacific Analyzer flow injection auto analyzer at the University of Wisconsin Center for Limnology. Ammonium samples were analyzed via the Automated Phenate Method (4500-$NH_3$H) and nitrate via the Automated Cadmium Reduction Method (4500-$NO_3$–F) (Franson, 1985). SRP samples were analyzed on a spectrophotometer via the Ascorbic Acid Method (4500-PE). Limitation of detection (LOD) for ammonium sample processing was 3 μg/l and nitrate LOD was 2 μg/l on the Astoria Pacific analyzer. LOD for SRP on the spectrophotometer was 0.5 μg/l. Values below the LOD for these analytes were assigned half the LOD value (ammonium—1.5 μg/l; nitrate—1 μg/l; SRP—0.25 μg/l). Because approximately one third of the ammonium samples were below the LOD, they were omitted from this study (see Fuller (2009) for details.)

To evaluate the effects of beaver ponds on nutrient concentrations, the ratio of downstream to upstream concentrations was calculated for each pond. Ratios of response variables were used where possible, because they standardize the spatial changes by the ambient background conditions of each reference (upstream) reach, and thereby provide a more comparable measure of relative effects. If significant changes were observed from upstream to downstream of beaver ponds, then ratios of upstream/spillover nutrient concentrations and spillover/downstream nutrient concentrations were also compared to evaluate the potential for pond spillover nutrients to augment or dilute downstream nutrient inputs from groundwater.

## Nutrient limitation

Nutrient diffusing substrates (NDS) were deployed upstream and downstream at 10 sites in 2008 to test for effects of beaver ponds on nutrient limitation of periphyton (Tank & Dodds, 2003). NDS were incubated in streams for 17 days and glass frits were frozen in film canisters for chlorophyll $a$ extraction (see chlorophyll $a$ analysis for benthic periphyton below). Eight replicates of four treatments (+Nitrogen (N), +Phosphorus (P), +Nitrogen and Phosphorus (N + P) and a Control (C)) were deployed in each reach. Nutrient augmentation was made using $NaNO_3$ for nitrogen additions and $KH_2PO_4$ for phosphorus additions. Nitrogen and phosphorus augmentations were both added to agar at a 0.5 M concentration. A two-way analysis of variance was used to test for limiting nutrients in each stream reach (Tank & Dodds, 2003).

To determine if the overall magnitude of nutrient limitation was different upstream and downstream of beaver ponds, a relative response ratio was calculated for each reach by dividing mean algal biomass from the NDS glass frits for the limiting nutrient (N, P or N + P (co-limitation)) by the mean algal biomass accrued on the control (Francoeur, 2001). For each pond, response ratios were compared by subtracting the upstream from the downstream response ratios. A positive difference in response ratios indicates greater nutrient limitation downstream and a negative difference indicates less nutrient limitation downstream.

### Benthic and pond spillover algae biomass as basal resources for consumers

Biomass of benthic algae in the upstream and downstream reaches was estimated to determine if beaver ponds altered food resources for grazing invertebrates. On one date (4–5 August) during summer 2008 10 rocks were randomly collected from upstream and downstream of each beaver pond and frozen for future analysis. Rocks were completely extracted (submerged) in 90% $MgCO_3$-buffered ethanol. Extracts were analyzed fluorometrically to estimate chlorophyll *a* concentration according to EPA Method 445.0 (Arar & Collins, 1997). Extracted rocks were traced on paper and the paper cutouts were scanned with a LI-COR LI-3100C area meter (0.1 $mm^2$ resolution and an accuracy of ±1%) to estimate the two-dimensional area of streambed occupied by each rock. Rock areas ranged from ~15 to 65 $cm^2$. Rock areas were used to estimate a mean algal biomass per unit area (mg chlorophyll *a*/$m^2$) in each reach.

Five pond spillover phytoplankton samples were collected at each site on 16–21 July 2008 as a potential food resource (seston) for suspension-feeding invertebrates by filtering 1 l of pond spillover water through a 0.7 μm pore size Whatman glass microfiber filter. Filters were frozen and later extracted and analyzed fluorometrically by methods described above. Spillover chlorophyll *a* concentrations were transformed (ln($x$)) to meet normality assumptions.

### Benthic organic matter as a basal resource for consumers

To evaluate changes in benthic organic matter (BOM) between upstream and downstream reaches, five replicate BOM samples were collected once during summer 2008 (16–21 July) at 10 sites. A bottomless 18.9-l bucket was used to isolate a known area (0.05 $m^2$) of stream bottom by burying the edge into the stream substrate effectively sealing the streambed and associated BOM within the bucket. Average water depth in the bucket was measured to estimate the total volume of water in the bucket. The BOM was homogeneously suspended into the water by gently disturbing the substrate. The BOM-water slurry was then sub-sampled and filtered onto a pre-ashed and pre-weighed 47 mm Whatman glass microfiber filter with a pore size of 0.7 μm. Filters were frozen for 1–2 months and then dried in a drying oven at 60°C until there was no weight change, ashed in a muffle furnace at 450°C for 2 h and weighed again to calculate the ash-free-dry-mass (AFDM). Using the known volume of water in the bottomless bucket, sub-sample volume filtered and area of stream bottom, a BOM AFDM per unit area (g AFDM/$m^2$) of stream bottom was calculated. Natural log transformation of BOM AFDM was required to meet normality assumptions.

### Invertebrate communities

Benthic invertebrate samples were collected once (21–22 July) during summer 2008 to characterize the primary consumer communities of the upstream and downstream reaches at each beaver pond site. Samples were collected using a 30-s kick sample that covered one complete transect of the stream. To minimize disturbance of the habitat, only one set of BOM and benthic invertebrate samples were taken downstream of CMC5 and upstream of CMC4 because of the relatively short distance between those two ponds. Samples were sorted in the field and preserved in 70% ethanol. Abundance was compared among sites as catch per unit effort (30 s). Invertebrates were identified to lowest practical taxonomic unit (usually genus or species) and categorized into functional feeding groups (FFG) (collector-gatherers, grazers, predators, shredders, and suspension-feeders). Invertebrates from the family Chironomidae were not included in this analysis due to high variability in functional feeding groups among species within the family. Preliminary benthic samples taken in summer 2007 indicated that Chironomidae occupied from 9 to 64% of the total community

abundance in streams of this region (Fuller, 2009). In 2008, chironomid abundance was very low in the study streams due to a combination of high flows and low population levels of the nuisance diatom, *Didymosphenia geminata* (unpublished observations). Therefore, the analysis of FFGs included at least 90% of the benthic invertebrate numbers in the samples, and even a higher percentage of the invertebrate biomass because of the small size of chironomids.

Effects of beaver ponds on benthic invertebrate consumers were evaluated by comparing ratios of abundances for each FFG (downstream/upstream) and testing whether pond morphology predicted variation in those ratios. Shredders and collector-gatherers were combined into one group (detritus-feeders) for analyses, because the benthic organic matter (BOM) samples were not fractionated by size, thereby including resources for both groups. Invertebrate abundance data were natural log transformed ($\ln(x + 1)$) accordingly to meet normality assumptions.

### Statistical analyses

Two approaches were used to evaluate beaver pond effects on downstream reaches. First, one-sample $t$ tests evaluated whether there were systematic increases or decreases in each parameter downstream of all beaver ponds compared to their upstream reference reaches. $T$ tests were conducted on the ratios of downstream/upstream measurements with a null hypothesis of $\mu = 1$ (or $\mu = 0$ if the ratio was log transformed to meet normality assumptions assessed by Lillifors tests for normality). Rejection of the null hypothesis indicated that a response variable systematically increased or decreased downstream of beaver ponds.

If the $t$ test resulted in failure to reject the null hypothesis, indicating a lack of systematic effects of beaver ponds on response variables, then linear regression was used to test whether variation in the pond morphology ratio (ln(dam height/pond surface area)) as the independent variable was related to variation in the downstream/upstream response variable ratios.

In regression analyses, Cook's Distance values were used to identify data points as outliers (Cook's Distance greater than 0.5). Occasional outliers were removed from regression analyses and resulted in variation in the number of degrees of freedom among analyses. No one stream or site produced consistent outliers; therefore, the criterion for outlier omission was strictly statistical. Contaminated samples were also removed from the analyses. All statistical analyses were conducted in R (R Development Core Team, 2008).

## Results

### Effects of beaver ponds on stream water nutrient concentrations

Stream water nutrient concentrations were generally very low, as has been observed in other studies of streams of this region (Peckarsky et al., 2001). Soluble reactive phosphorus (SRP) was higher and had greater variability during the low-flow year (2007) than during the high-flow year (2008) ranging from below detection limits (BDL) to 11.5 μg/l in 2007, and from BDL to 1.2 μg/l in 2008 (Table 1). Similarly, nitrate achieved higher concentrations and had a greater range of concentrations during the low-flow year (6.2–138.2 μg/l) versus the high-flow year (4.7–85.2 μg/l) (Table 1). In contrast, ranges of ammonium concentrations were similar between low- (BDL to 9.6 μg/l) and high-flow years (BDL to 20.9 μg/l) (Fuller, 2009). Note that results for SRP should be interpreted with caution, because some samples were below the level of detection, especially in 2008 (Table 1).

There were no systematic increases or decreases in SRP concentrations from upstream to downstream of beaver ponds in either year (4 $t$ tests; $P > 0.05$). However, nitrate concentrations (mean difference ± SE) were significantly higher downstream of beaver ponds in the low-flow year (2.76 ± 0.96 μg/l) ($t$ test, $t_{(11df)} = 5.67$, $P = 0.0001$). Nitrate concentrations in the high-flow year did not differ upstream versus downstream of beaver ponds ($t$ test, $t_{(9df)} = 0.60$, $P = 0.6$). SRP ratios were significantly predicted by pond morphology during the low-flow year (2007, $t_{(9df)} = 2.96$, $P = 0.02$), but not the high-flow year (2008, $t_{(8df)} = -1.23$, $P = 0.3$) (Fig. 2). Thus, during the low-flow year, SRP concentrations increased downstream of high-head, small surface area beaver ponds and decreased downstream of low-head, large surface area ponds. Non-significant

**Table 1** Summary of concentrations of soluble reactive phosphorus (SRP) and nitrate-N ($NO_3$-N) from each site

| Site | Year | Pond morphology ratio | SRP (μg/l) | | | $NO_3$-N (μg/l) | | |
|---|---|---|---|---|---|---|---|---|
| | | | Down | Spill | Up | Down | Spill | Up |
| WBC1 | 2007 | 3.2 | 0.7 | 0.9 | 0.5 | 138.2 | 137.6 | 135.0 |
| WBC2 | 2007 | 3.3 | 0.8 | 0.6 | *0.25* | 103.5 | 100.8 | 96.8 |
| WBC4 | 2007 | 2.8 | 0.7 | *0.25* | 0.6 | 134.2 | 128.3 | 121.4 |
| WBC5 | 2007 | 1.7 | 0.7 | 1.2 | 3.2 | 127.2 | 128.2 | 126.5 |
| CC1 | 2007 | 2.3 | 4.8 | 3.7 | 6.3 | 19.2 | 18.2 | 16.9 |
| CC2 | 2007 | 3.1 | 11.5 | 9.2 | 9.4 | 12.7 | 11.7 | 11.5 |
| EBC1 | 2007 | 1.7 | (5.3) | (0.6) | (*0.25*) | 15.9 | 15.7 | 15.4 |
| EBC3 | 2007 | 1.2 | *0.25* | 0.5 | 0.5 | 25.7 | 30.5 | 24.9 |
| EBC4 | 2007 | 2.2 | *0.25* | *0.25* | 0.5 | 30.4 | 30.7 | 29.5 |
| OBJ1 | 2007 | 1.9 | 0.8 | 1.0 | 0.5 | 6.8 | 12.1 | 6.2 |
| OBJ2 | 2007 | 0.9 | 0.6 | *0.25* | 1.0 | 7.7 | 7.6 | 7.2 |
| OBJ3 | 2007 | 2.1 | 0.7 | 0.9 | 0.8 | 7.3 | 7.9 | 6.6 |
| WBC1 | 2008 | 3.2 | 0.7 | 0.6 | 0.5 | 85.2 | 78.3 | 78.4 |
| WBC2 | 2008 | 4.1 | 0.7 | 0.8 | 1.0 | 69.0 | 71.4 | 70.8 |
| WBC4 | 2008 | 4.1 | 1.0 | 1.0 | 1.0 | 74.2 | 75.0 | 74.2 |
| WBC5 | 2008 | 1.5 | 1.2 | 1.3 | 0.9 | 80.0 | 80.9 | 80.2 |
| CMC1 | 2008 | 2.9 | 1.2 | 0.9 | 0.6 | 15.4 | 16.0 | 16.6 |
| CMC2 | 2008 | 2.2 | 0.8 | 0.7 | 0.6 | 14.7 | 14.6 | 14.5 |
| CMC3 | 2008 | 2.6 | 0.8 | *0.25* | 0.7 | 4.7 | 4.6 | 5.1 |
| CMC4 | 2008 | 4.1 | 0.6 | 3.0 | 0.5 | 37.6 | 36.3 | 35.5 |
| CMC5 | 2008 | 4.2 | *0.25* | 0.5 | *0.25* | 33.5 | 32.7 | 29.3 |
| CMC6 | 2008 | 3.5 | *0.25* | *0.25* | 0.85 | 23.6 | 22.4 | 23.2 |

Site acronyms are West Brush Creek (WBC), Coal Creek (CC), East Brush Creek (EBC), Oh-Be-Joyful Creek (OBJ), and Cement Creek (CMC). Pond morphology ratio is ln(dam height (m)/pond area (ha)). Values in parentheses were outliers not used in regression analyses (see Fig. 3). Values in italics were below detection and represent the assigned value (SRP—0.25 μg/l) as described in the "Materials and methods" section

regressions of pond morphology and SRP ratios between upstream/spillover ($t_{(9df)} = -1.87$, $P = 0.09$) and spillover/downstream ($t_{(9df)} = -0.65$, $P = 0.5$) for the low-flow year suggested that spillover water neither augmented nor diluted stream water SRP downstream.

## Effects of beaver ponds on nutrient limitation

Nutrient diffusing substrates revealed high variability of limiting nutrients among sites. In three of the 10 sites there was no difference in nutrient limitation between the up and downstream reaches (Table 2); in all three cases both nitrogen and phosphorus were limiting (co-limitation). Of the remaining sites, two changed from co-limitation upstream to phosphorus limitation downstream; two changed from nitrogen limitation upstream to co-limitation downstream; and two changed from co-limitation upstream to nitrogen limitation downstream. One site was eliminated from the analysis because upstream NDS substrates were covered by bed movement.

The mean difference in phosphorus limitation response ratios between upstream and downstream reaches was −0.11 with 95% confidence intervals spanning −0.27 to 0.05. Those differences in phosphorus limitation response ratios indicated no systematic effects of beaver ponds on phosphorus limitation ($t$ test, $t_{(8df)} = -1.55$, $P = 0.2$). Furthermore, pond morphology did not significantly predict upstream–downstream differences in phosphorus limitation response ratios (regression, $t_{(7df)} =$

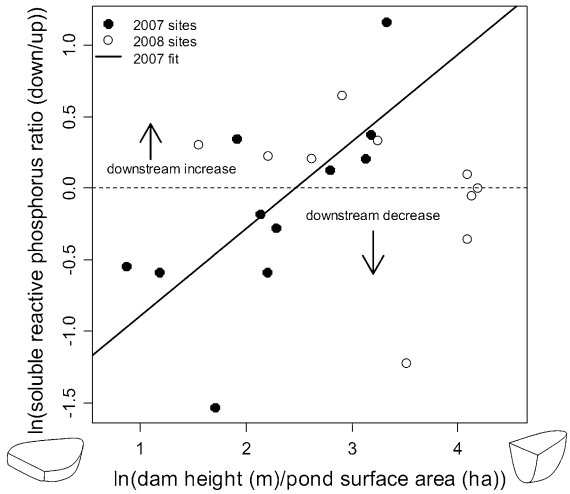


**Fig. 2** Relationships between beaver pond morphology ratios (ln (dam height/pond surface area)) and soluble reactive phosphorous (SRP) ratios (downstream concentration/upstream concentration) in 2007 (low-flow year) and 2008 (high-flow year), respectively. Data points above the *dashed line* indicate an increase in SRP downstream of beaver ponds and data points below the *dashed line* indicate a decrease in SRP downstream of beaver dams. *Regression line* indicates significant coefficient

$-0.54$, $P = 0.6$). Similarly, there was no systematic effect of beaver ponds on nitrogen limitation (response ratio differences: $t$ test, $t_{(8df)} = 0.48$, $P = 0.6$), and beaver pond morphology did not significantly predict changes in nitrogen limitation downstream (regression, $t_{(7df)} = -0.50$, $P = 0.6$).

## Effects of beaver ponds on basal resources

One sample $t$ tests indicated that neither algal biomass nor BOM changed systematically from upstream to downstream of beaver ponds (algae: $t_{(8df)} = -1.80$, $P = 0.1$; BOM: $t_{(7df)} = 1.62$, $P = 0.1$). After the removal of one statistical outlier (Cement Creek Site 3), there was a significant negative relationship between pond morphology and relative algal biomass (regression, $t_{(6df)} = -3.94$, $P = 0.008$) suggesting that algal biomass decreased downstream of high-head, small surface area ponds and increased downstream of low-head, large surface area ponds (Fig. 3a). Similarly, BOM AFDM decreased downstream of high-head ponds and increased downstream of low-head, large surface area ponds, as indicated by a significant negative relationship between the beaver pond morphology ratio and BOM AFDM ratios (downstream BOM AFDM/upstream BOM AFDM) (regression, $t_{(6df)} = -2.54$, $P = 0.04$) (Fig. 3b). In contrast, pond spillover phytoplankton was not related to pond morphology (regression, $t_{(8df)} = 0.33$, $P = 0.8$) (Fig. 3c), suggesting that pond morphology does not explain variation in spillover-water phytoplankton.

**Table 2** Summary of limiting nutrients as indicated by the nutrient diffusing substrate experiment in 2008 (N—nitrogen limited, P—phosphorus limited, CO—nitrogen and phosphorus limited); benthic organic matter ash-free dry mass; benthic and pond spill-over water chlorophyll *a* concentration

| Site | NDS limiting nutrient | | BOM AFDM (g/m$^2$) | | Benthic algae chl *a* (mg/m$^2$) | | Pond chl (μg/l) |
|---|---|---|---|---|---|---|---|
| | Up | Down | Up | Down | Up | Down | |
| WBC1 | CO | N | 10.90 | 8.49 | 4.32 | 4.86 | 0.079 |
| WBC2 | | P | 1.47 | 2.06 | 3.41 | 2.71 | 0.072 |
| WBC4 | CO | P | 3.56 | 4.30 | 3.93 | 2.31 | 0.077 |
| WBC5 | CO | P | 2.99 | 12.15 | 2.82 | 2.75 | 0.095 |
| CMC1 | N | CO | 8.86 | 11.30 | 2.53 | 2.34 | 0.106 |
| CMC2 | N | CO | 7.34 | 24.99 | 2.74 | 3.26 | 0.094 |
| CMC3 | CO | CO | 6.83 | 8.74 | 3.25 | 1.92 | 0.212 |
| CMC4 | CO | N | (76.81) | (4.53) | 9.29 | 5.70 | 0.173 |
| CMC5 | CO | CO | (5.26) | (76.81) | (3.25) | (9.72) | 0.193 |
| CMC6 | CO | CO | 13.13 | 8.45 | 2.94 | 2.84 | 0.218 |

Values in parentheses were outliers not used in regression analyses, and blanks indicate no data. Site acronyms as in Table 1

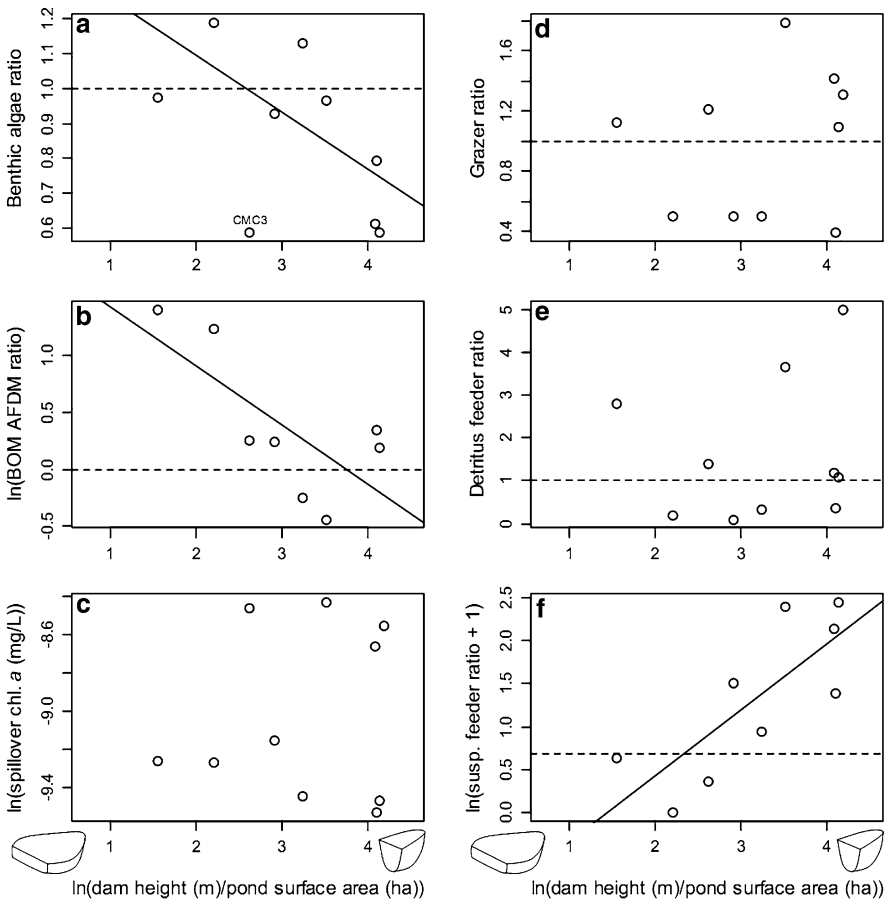


**Fig. 3** Relationships between beaver pond morphology ratios (ln(dam height/pond surface area)) and downstream/upstream ratios of **a** benthic algae chlorophyll *a*, **b** benthic organic matter (BOM) ash-free dry mass (AFDM), **c** spillover water chlorophyll *a* concentration, **d** catch per unit effort of grazing invertebrates, **e** catch per unit effort of detritus-feeding invertebrates, and **f** catch per unit effort of suspension-feeding invertebrates. Data points above the *dashed lines* indicate an increase in that variable downstream of beaver ponds and data points below the *dashed lines* indicate a decrease downstream of beaver ponds. Significant predictions of response variables by pond morphology are indicated by the presence of a *regression line*

### Effects of beaver ponds on benthic invertebrate functional feeding groups

Non-chironomid grazer abundances were almost entirely (99.6%) comprised of mayflies from the families Baetidae and Heptageniidae. Furthermore, predators were mostly (75%) large stoneflies of the family Perlodidae. A majority (55%) of the detritus consumers were small stonefly shredders from the Nemouridae family, while 90% of the suspension feeder abundance was accounted for by the family Simuliidae.

One sample *t* tests on the abundance ratios (natural log transformed ($\ln(x + 1)$) for suspension feeders) showed that the abundance of none of the invertebrate functional feeding groups changed systematically between upstream and downstream of beaver dams (response ratios not significantly different from zero (suspension feeders: $t_{(8df)} = 2.08$, $P = 0.07$; grazers: $t_{(9df)} = -0.10$, $P = 0.9$; predators: $t_{(9df)} = 0.59$, $P = 0.6$; detritus feeders: $t_{(9df)} = 1.16$, $P = 0.3$). Furthermore, there were no significant regressions between pond morphology and the downstream/upstream ratios of grazers, predators or detritus feeders (grazers: $t_{(8df)} = 0.56$, $P = 0.6$; predators: $t_{(8df)} = 0.52$, $P = 0.6$; detritus feeders: $t_{(8df)} = 0.41$, $P = 0.7$) (Fig. 3d, e). However, a positive relationship between pond morphology and the downstream/upstream ratio of suspension feeders (regression, $t_{(7df)} = 3.31$, $P = 0.01$) indicated that their abundance increased downstream of high-head, small surface area ponds and decreased downstream of low-head, large surface area ponds (Fig. 3f).

## Discussion

This study demonstrates that beaver ponds had very few systematic effects on downstream ecosystems. Instead, the effects of beaver ponds on downstream

nutrients, basal resources and invertebrate consumers were highly variable and depended on beaver pond morphology and annual hydrologic variation. For example, nitrate concentration increased significantly downstream of beaver dams, but only during baseflow conditions. Soluble reactive phosphorus (SRP) increased downstream of high hydraulic-head dams and decreased downstream of low-head dams, but also only during baseflow conditions. While beaver pond morphology predicted variation in the downstream abundance of some basal resources (periphyton biomass and benthic organic matter decreased downstream of high-head dams and increased downstream of low-head dams), variation in others was not explained by beaver pond morphology (pond spillover chlorophyll *a*). Additionally, pond morphology affected the abundance of suspension-feeding benthic invertebrates (increased downstream of high-head dams and decreased downstream of low-head dams), but not that of periphyton grazers or detritus consumers.

Previous experiments describing phosphorus dynamics in wetland sediments have shown that sorption to sediments is the primary process removing SRP from the water column, while microbial biofilm and vegetation uptake are of lesser importance (Lantzke et al., 1998). No submerged or emergent aquatic macrophytes were observed at the study sites; so the driving mechanisms for SRP retention and release in this study were likely either sorption on sediments and/or microbial uptake (algae on pond sediments included).

Hydrology has been shown to drive SRP transport in some wetland systems (Schulz & Herzog, 2004; Reinhardt et al., 2005). In fact, other studies have found extreme changes in discharge to result in nutrient sources becoming nutrient sinks (Stanley & Boulton, 1995). The contrast in SRP concentrations and different relationships between SRP and pond morphology observed during low and high water years may be explained similarly by extreme differences in hydrology. The study sites experienced a very dry winter in 2007, and therefore reached baseflow conditions much earlier (late June–early July) than in 2008 (mid August). A multi-year drought was interrupted in winter 2007–2008 with more snow than any year since the 1996–1997 winter and resulted in snowmelt runoff that remained high late into the summer. Therefore, 2007 water samples were collected after baseflow conditions had been achieved for more than 3 weeks, but 2008 samples were collected before snowmelt flows had completely receded. Therefore, dilution of SRP was likely the cause of the very low concentrations measured in 2008.

Extreme differences in hydrological conditions between years may have altered the relative effects of upwelling groundwater and spillover surface water on the nutrient concentrations of the downstream reaches. After a sustained period of baseflow conditions (as in 2007) small surface area ponds with high-head dams (high morphology ratios) have greater hydraulic head gradients driving upwelling into downstream reaches relative to larger surface area ponds with low-head dams (Boano et al., 2008). The extremely low concentrations of SRP in the stream surface waters makes it plausible that SRP traveling through groundwater, although generally at low concentrations, could substantially augment the ambient stream surface water concentrations downstream of high-head ponds even after uptake by benthic algae at the sediment surface (Dent et al., 2001; Hunt et al., 2006). After an extended period of high flow conditions (as in 2008), the upwelling SRP signal may be diluted by runoff and the nutrient concentrations would reflect surface water chemistry rather than groundwater chemistry. More extensive analyses of SRP concentrations in groundwater and spillover water of beaver ponds during high and low flow years are needed to rigorously test this hypothesis.

In contrast, nitrate concentrations in the low-flow year were significantly higher downstream of beaver ponds, but were not related to pond morphology. Since there were no relationships between downstream and pond spillover nitrate concentrations, nitrification in the hyporheic zone as proposed by Jones et al. (1995), might explain the greater concentrations downstream where upwelling is hypothesized to be greatest (Coleman & Dahm, 1990). Genereux et al. (2008) determined that stream substrate hydraulic conductivity increased downstream of beaver ponds. They hypothesized that such increased hydraulic conductivity would result in the consistent transport of nitrate from the hyporheic zone to the surface waters. Although the effects of beaver ponds on downstream nitrate concentrations were systematic during baseflow conditions, it is unclear whether the small magnitude of the increase

in nitrate concentration (<3 μg/l) downstream of beaver ponds would be ecologically important. Furthermore, high water dilution of any groundwater nitrate inputs could explain why no systematic increase in nitrate concentration was observed downstream of beaver ponds during the high-water year.

Results showed that the biomass of benthic algae was altered by pond morphology during the high-flow year. In specific, algal biomass was reduced downstream of high-head dams and increased downstream of low-head dams. This pattern could not have been explained by nutrient limitation, which was not related to pond morphology or benthic algal biomass. Other potential mechanisms controlling algal biomass could be grazing invertebrates (Taylor et al., 2002; Álvarez & Peckarsky, 2005) and hydrologic scouring (Francoeur & Biggs, 2006). However, there was no apparent relationship between grazer abundance and algal biomass under the high water conditions when samples were taken in 2008. At baseflow conditions, hydrologic disturbance is dampened in reaches downstream of beaver dams (Meentemeyer & Butler, 1999). However, it is possible that hydrologic scouring could have reduced algal standing stock downstream of higher-head beaver ponds during an extreme hydrologic year, such as 2008.

The influence of beaver ponds on BOM dynamics may have large consequences for detrital food webs if this resource varies with beaver pond morphology. In South America, the contribution of BOM as energy for secondary production was 100–200% greater downstream of beaver ponds when compared to reference reaches (Anderson & Rosemond, 2010). However, BOM has been shown to accumulate upstream of human-constructed impoundments (Ward & Stanford, 1983). In a study of two constructed wetlands, the size and shape of the wetland were important predictors of total suspended solid transport through the wetland (Koskiaho, 2003). Interestingly, our results showed a negative, however weak, relationship between pond morphology and benthic organic matter ash-free dry mass. Standing stock of BOM was higher downstream of low-head dams (Fig. 3b) suggesting that ponds with lower dams and larger surface areas are less retentive of particulate organic matter than ponds with high dams and small surface area. Again, the extreme hydrologic conditions during the 2008 sampling period might have dampened the observed pattern because high flows often carry large loads of suspended organic matter (Francoeur & Biggs, 2006). BOM samples were taken during the descending limb of spring snowmelt while discharge was still high, and therefore more benthic organic matter would be transported to downstream reaches of all dams, obscuring the effects occurring under baseflow conditions.

No functional feeding groups (FFG) of invertebrates varied systematically downstream of beaver dams, but the suspension feeders varied predictably with pond morphology. Overwhelming evidence from man-made reservoirs and lakes shows widespread increases in abundance of suspension feeders downstream of the reservoirs and in lake outlets (e.g., Mackay & Waters, 1986; Richardson & Mackay, 1991). Previous studies have similarly documented increases in suspension feeding invertebrates downstream from beaver ponds (Clifford et al., 1993; Margolis et al., 2001a; Anderson & Rosemond, 2007). The hypothesized mechanism for this response is that lakes, reservoirs, and ponds promote phytoplankton growth and therefore increase the flux of high quality food resources for suspension feeders (Richardson & Mackay, 1991). Despite such evidence from other stream–pond–stream habitats, a systematic increase in suspension feeders downstream of all beaver ponds was not observed in this study. Furthermore, the abundance of suspension feeders downstream of beaver ponds was not related to the biomass of algae spilling over the dam. These results run counter to those of other studies and suggest that suspension feeders may be tracking a food source other than phytoplankton (Fuller & Fry, 1991) that is not systematically greater downstream of ponds.

Simuliidae, the dominant suspension feeders of the study, have been known to feed on bacteria and to grow at faster rates while feeding on cultured bacteria when compared with other potential food sources (Fuller & Fry, 1991). It is possible that higher abundance of Simuliidae downstream from high-head dams could be explained by greater availability of bacterial seston. Alternatively, black fly larvae have been shown to thrive at higher scour locations (Hemphill & Cooper, 1983), which may predominate downstream of the high dams under high flow conditions.

Hydrologic variation has been discussed widely as a mechanism shaping aquatic ecosystems (Poff et al., 1997). High flows can dilute nutrients or pulse

nutrients from the landscape (Pringle et al., 1988), reduce algae via scouring (Francoeur & Biggs, 2006) and alter abundance and richness of benthic invertebrates (Holomuzki & Biggs, 1999; Wagner & Schmidt, 2004). The high water conditions experienced in 2008 may have resulted in lower variability of all parameters measured (homogenization of the entire system) and therefore reduced the probability of detecting effects of beaver pond presence and morphology on downstream food webs. A robust test of the influence of variation in hydrologic regime on the downstream effects of beaver ponds requires replication of this study under multiple low and high flow years.

## Conclusions

This study demonstrates that beaver-engineered impoundments do not have systematic effects on downstream ecosystems. Variation in the effects of beaver ponds on some stream nutrients, basal resources and invertebrate consumers may be predicted by observing beaver pond morphology. However, pond morphology does not provide a universal mechanism explaining the widespread variation in effects of beaver altered systems on downstream ecosystems. Our results show that annual hydrologic variation can strongly influence not only the rare systematic effects, but also the effects of pond morphology on downstream ecosystems. Beavers impound much smaller waterways than most human-constructed impoundments or natural lakes. Therefore, only limited extrapolation from human impoundments and natural lake systems can be made to beaver ponds. Therefore, a new conceptual framework focusing on smaller temporal and spatial scales is needed to describe the importance of beaver impoundments and the variation of their effects on streams and the landscape.

**Acknowledgments** We would like to thank the following people for help in the field, lab and statistical consultation: Brad Taylor, Wendy Brown, Jen Moslemi, Marge Penton, Steve Horn, Grace and Randy Fuller, Janelle Bossé, Maruxa Álvarez, Claudio Gratton, Steve Loheide, Scott Wissinger, Angus McIntosh, Niki Stone, Carrie Robbins, Alison Horn, Alexis Drutchas, Sandye and Oakleigh Adams. Comments from Wyatt Cross, Emily Stanley, Emily Bernhardt and two anonymous reviewers improved earlier drafts of the paper. We especially acknowledge the contribution of Stanley Dodson as a key mentor to both authors. Stanley always encouraged us to embrace unexpected, conflicting or counterintuitive results, which provide the basis for making new discoveries. This research was supported by the University of Wisconsin (Graduate Research Grants, Anna Grant Birge Memorial Award), the Rocky Mountain Biological Laboratory, Colorado Mountain Club Foundation, the American Museum of Natural History and NSF grant DEB-0516035 to B. L. Peckarsky.

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