

BEAVER POND MORPHOLOGY AS A TOOL FOR PREDICTING
CHANGES DOWNSTREAM

by

Matthew R. Fuller

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APPROVED BY:

Dr. Barbara L. Peckarsky
University of Wisconsin-Madison
Zoology Department

AND

Dr. Emily H. Stanley
University of Wisconsin-Madison
Center for Limnology

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Beaver pond morphology as a tool for predicting changes downstream

Matthew R. Fuller

Under the supervision of Professor Barbara L. Peckarsky

and Emily H. Stanley

At the University of Wisconsin – Madison

It is believed that beaver, *Castor* (Castoridae), have been altering their environment for as many as 24 million years. Their impacts on both lotic and lentic environments have developed research programs in a diversity of disciplines including biogeochemistry, ecology, evolution, geomorphology, hydrology and limnology. Habitat modification, as a direct result from beaver activity, has strong implications for adjacent ecosystems and is an important driver of patch diversity at the landscape scale. The effects of beaver ponds, bank burrows, and island lodges can also be felt beyond the immediate physical disturbance which can extend the boundary of beaver modification from pond edges to the upland hills and downstream to lower reaches.

Impacts on beaver pond tail waters are one of the most heavily studied effects of beaver habitat modification. The literature suggests a wide variety of effects can be measured downstream of beaver ponds ranging from changes in physical characteristics of stream substrate, hydrology and water temperature to biotic components including primary production and animal communities. From these previously described effects, studies have

reported results with inconsistent directional changes in downstream reaches. When discussing these varied results, often only site-specific mechanisms are identified from the different studies. This lack of synthesis offers no generalities to the effects that beaver ponds have on their downstream reaches.

The major objective of this work was to evaluate if beaver pond morphology (pond size and shape) could be used as a predictor to explain some of the variation in downstream alterations. Chapter one focused on the change in stream water temperature from above to below beaver ponds and how that temperature change related to pond morphology. I found that ponds with high hydraulic-head dams and smaller surface areas had lower water temperature downstream (when compared to the upstream reference reach) and ponds with low hydraulic-head dams and large surface areas had higher water temperature downstream. Temperature is known to control many biological processes in aquatic habitats and therefore the change in temperature associated with beaver ponds was evaluated with regards to its impact on stream mayfly size and development above and below beaver ponds. Beaver pond morphology significantly predicted mature *Baetis bicaudatus* nymph size in downstream reaches. Larger *B. bicaudatus* were collected downstream of ponds with high-head dams and small surface areas (cooling ponds) and smaller individuals were collected downstream of ponds with low-head dams and large surface areas (warming ponds). It was hypothesized that the changes in size were associated with the relationship between water temperature and development period (cooler temperature = longer development period leading to larger size at maturity; warmer temperature = shorter development period leading to smaller size at

maturity), but evaluation of *B. bicaudatus* peak emergence timing between up- and downstream reaches did not support this prediction.

Chapter two focused on invertebrate communities and their associated lower trophic levels above and below beaver ponds. Stream water nutrients, nutrient limitation, benthic algae, benthic organic matter, and invertebrate communities were described up- and downstream of 10 beaver ponds and evaluated for either a consistent change downstream or a relationship to pond morphology. Only nitrate concentrations during one sampling season (2007) demonstrated a consistent change (nitrate increased) downstream of all beaver ponds. Ammonium, soluble reactive phosphorus (SRP), phosphorus and nitrogen limitation, benthic algae, benthic organic matter, and all invertebrate functional feeding groups (detritus feeders, grazers, predators, and suspension feeders) did not demonstrate a consistent increase or decrease downstream of all beaver ponds. However, SRP, benthic algae, benthic organic matter and suspension feeding invertebrates all demonstrated a significant relationship with pond morphology. SRP concentration and suspension feeder abundance were higher downstream of high-head dams and benthic algae and benthic organic matter were lower downstream of high head dams.

The diverse effects beaver ponds have on their downstream reaches is nothing new. However, the attempt to organize those effects and identify predicting variables of the downstream alterations is an exciting area of research. This work has taken an initial stab at explaining some of the variation among the many downstream effects beaver ponds have on their tail waters. Nevertheless, further investigation across larger pond morphology gradients

and wider geographical regions is necessary before a thorough understanding of the capacity for beaver pond morphology to be used as a tool for predicting alterations downstream.

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Chapter 1

Beaver pond morphology predicts downstream water temperature and mayfly size

Abstract

As natural discontinuities of stream networks, beaver ponds have the potential to influence the structure and function of stream ecosystems. After declining during the extensive fur trade in North America, beaver populations have recently grown in some areas, especially montane regions. While previous studies have documented a variety of effects of beaver ponds on stream tail waters, little is known about the mechanisms driving those effects and no consistent generalities have emerged. I studied 18 montane beaver ponds of varying size and shape in western Colorado near the Rocky Mountain Biological Laboratory. Our goal was to test whether variation in beaver pond morphology (pond size and shape) explains downstream changes in stream temperature, mayfly size and timing of emergence.

Downstream water temperatures varied predictably with pond morphology, being colder downstream of high-head dams and warmer downstream of low-head dams. Pond morphology also significantly predicted variation in size of mature *Baetis bicaudatus* (the most abundant mayfly), with larger mayflies emerging downstream of high-head dams and smaller mayflies downstream of low-head dams. There was no relationship between pond morphology and variation in timing of emergence of *Baetis* between up- and downstream

reaches. Multiple linear regression showed that none of the potential mechanisms tested (predatory stonefly abundance, food resource availability and stream temperature) explained the relationship between pond morphology and mayfly size. Our results have interesting implications for the effects of beaver ponds on *Baetis* individual fitness, because large *Baetis* females are more fecund. Furthermore, predictable female size variation associated with beaver pond morphology makes it possible to model the effects of beaver activity on local contributions of *Baetis* to the regional pool of reproductive adults at the catchment scale.

Introduction

Beaver dams are naturally occurring discontinuities of the longitudinal flow of stream networks and were once ubiquitous across North American waterways (Bulter 1995; Naiman et al. 1988). Despite a historical decline in beaver populations throughout North America in the 1800s, they are currently rebounding (Naiman et al. 1988). Today, there are regions where as much as 40% of the overall stream length is affected by beaver dams (Hammerson 1994). Furthermore, beaver are an invasive species in South America where population growth is increasing at more than 20% per year (Lizarralde et al. 2004). The ponds created by beaver activity are relatively short-lived compared to reservoirs created by human-constructed dams; and the riverine habitats beaver create usually have more similarities to low gradient floodplain rivers (Naiman et al. 1988) or lentic systems (Anderson et al. 2009; Hammerson 1994) than to the low order streams that the dams impound (Jakes et al. 2007). Therefore, beaver activity alters the continuity of river environments from that predicted by the River Continuum Concept (Vannote et al. 1980) by inserting habitats similar to large

river ecosystems into low order streams. In addition, the nature of headwater stream networks has been shown to influence the larger rivers downstream (Gomi et al. 2002). This link suggests the effects of beaver activity could extend well beyond local influences near the pond to affect larger rivers. Thus, it is important to expand our understanding of beaver influences on headwater stream patterns and processes as beaver increase in number and occupy more waterways.

Previous studies have reported numerous differences between stream reaches upstream and downstream of beaver ponds. For example, beaver ponds may change groundwater flow patterns (Westbrook et al. 2006; White 1990), streambed substrate hydraulic conductivity (Genereux et al. 2008), water temperatures (Margolis et al. 2001a; Margolis et al. 2001b; Maxted et al. 2005; McRae and Edwards 1994), and the timing of aquatic insect emergence (Rolauffs et al. 2001). Higher water tables associated with beaver altered landscapes have also been found to significantly affect riparian plant growth and species composition surrounding the pond (Westbrook et al. 2006; Wright et al. 2002). Furthermore, elevated water tables cause changes in pressure heads of groundwater which can result in greater groundwater upwelling downstream of beaver dams (White 1990). Consequently, alteration in hydrology associated with pond-induced upwelling could cause cooler groundwater to influence downstream water temperatures (Hunt et al. 2006; White 1990). Those thermal modifications could affect insect development time and growth rates, thus altering life histories of insects in stream reaches downstream of beaver impoundments relative to their immediate upstream reaches (Ward and Stanford 1983).

Given that stream insects often use water temperature as a cue for emergence (Sweeney and Vannote 1978; Vannote and Sweeney 1980; Ward and Stanford 1982), changes in water temperatures associated with beaver altered streams could also affect the phenology of those insects. However, emergence of some stream insects is triggered by a change in temperature rather than by cumulative degree days (Ward and Stanford 1979). Consequently, an abrupt shift toward lower temperatures resulting from upwelling into the stream could cause delayed insect emergence downstream of beaver ponds. In contrast, the size and shape of a pond might allow it to receive more solar radiation reducing the influence of pond-associated upwelling on downstream water temperatures. Under this latter scenario, large surface area, low-head ponds could warm downstream reaches if warm pond water spills over the dam, resulting in completely opposite effects on insect development. Thus, expected effects on insect development downstream may vary depending on the size and shape of beaver ponds. Furthermore, accelerated development reduces the time for growth and can result in a smaller size at maturity when insects emerge from their aquatic habitats (Vannote and Sweeney 1980). Relatively small changes in female size will affect individual fitness if fecundity is related to size at maturity (Peckarsky et al. 1993).

The purpose of this study was to evaluate variation in beaver pond morphology as a predictor of differences in mayfly size and timing of emergence upstream and downstream of beaver ponds. I also evaluated various mechanisms to explain observed associations between beaver pond morphology and insect development. I tested the hypothesis that ponds with high dams (hydraulic head change) relative to pond surface area would be cooler downstream relative to upstream reaches and ponds with low dams relative to surface area would warm waters

downstream. I also tested whether those changes in temperature were associated with variation in the size of mayflies emerging from downstream reaches in comparison to upstream reaches. Specifically, I predicted accelerated development and therefore smaller emergence size of insects if temperatures warmed downstream of large surface area, low-head ponds and delayed development and larger emergence sizes of insects if temperatures cooled downstream of small surface area, high-head ponds.

Methods

Study Sites

In summers 2007 and 2008 I studied a variety of beaver ponds in Colorado, near the Rocky Mountain Biological Laboratory, to evaluate their impacts on stream water temperatures, insect size and timing of emergence in tailwaters downstream. Study sites in 2007 ($n = 12$) ranged in elevation from approximately 2800 - 3000 m and 2850 - 3150 m in 2008 ($n = 10$) (Table 1). Four sites in the West Brush Creek drainage were used in both 2007 and 2008. Beaver ponds in 2007 were located in 4 different drainage basins (Coal Creek (2), East Brush Creek (3), Oh-Be-Joyful Creek (3) and West Brush Creek (4)), while sites in 2008 were located in two drainage basins (Cement Creek (6) and West Brush Creek(4)). Sites consisted of a simple upstream reach – beaver pond – downstream reach geomorphic pattern (Fig. 1). This study site pattern was chosen to increase the probability of isolating the effects of a single pond on the downstream reach in comparison to a reference upstream reach. Thus, I collected all data in upstream reaches far enough upstream of beaver ponds to avoid any

influence of the pond itself. In 2007, hydraulic heights (measured as the distance from the water surface of pond to water surface of downstream reach; see Fig. 1) ranged from 0.28 – 1.77 m and 0.42 – 2.43 m in 2008. Surface areas of ponds ranged from 0.031 - 0.497 ha (2007) and 0.013 - 0.162 ha (2008) (Table 1). Pond lengths (linear distance from pond inlet to dam spillover; see Fig. 1) were generally short, ranging from 20 - 90 m (2007) and 15 - 50 m (2008), supporting the assumption that natural longitudinal change within a stream would have been minimal in the absence of the beaver pond (Table 1). Therefore, I attributed the observed differences between upstream and downstream reaches of a beaver pond to the presence of the pond. Measurements of pond surface area and all linear distances were made using a Thales ProMark3 GPS unit with an x-y plane accuracy of ± 1 cm and a elevational accuracy of ± 1 m. GPS data were analyzed using ArcMap 9.2.

I characterized each site by pond morphology. Measurements of hydraulic height, surface area, maximum pond width and pond length (Fig. 1) were evaluated with a principle components analysis (PCA) to determine which pond measurements were associated with the largest variation among sites (Fig. 2). Based on this PCA I described pond morphology as the natural log ratio of the beaver dam hydraulic height to pond surface area ($\ln(\text{hydraulic height (m)}/\text{pond surface area (ha)})$). This ratio was chosen because it incorporated both the variety of pond sizes and their relative depth. Additionally, this ratio should theoretically reflect variation in the potential influence of beaver ponds via groundwater inputs to downstream reaches (i.e. sites with low hydraulic heads and large surface areas should have less groundwater influence downstream than sites with high hydraulic head and small surface areas). I selected sites spanning a wide range of pond morphologies to increase the

probability of observing a relationship between pond size and shape and variation of downstream changes.

Stream temperature

Stream water temperature was recorded at locations both upstream and downstream of beaver ponds at each site in 2007 and 2008. Temperature was recorded every 5 minutes using Onset HOBO[®] Pendant Temperature/Light Data Loggers with a resolution of ± 0.1 °C. Although I installed the temperature loggers before baseflow was achieved in both 2007 and 2008, our analysis included only temperatures after baseflow was reached because the greatest groundwater influence would be expected during the baseflow period (Fig. 3). The baseflow period was determined by observing daily discharge at a USGS gauging station (09112200 – East River downstream of the confluence with Cement Creek), which was downstream of all study streams (Fig. 3). I calculated mean water temperatures for baseflow conditions at all sites in 2007 and 2008 and used each upstream reach as a reference. To analyze the effects of beaver pond morphology on stream temperatures, I subtracted the mean upstream from the mean downstream temperature, which resulted in positive temperature differences when the downstream reach warmed in comparison to the upstream reach. I used simple linear regression to test whether pond morphology predicted differences between mean baseflow water temperatures (downstream-upstream of beaver ponds) for 2007 and 2008 data independently.

Baetis bicaudatus size variation

To assess the effects of beaver ponds on aquatic insect development, I focused on the mayfly, *Baetis bicaudatus* Dodds (Baetidae), which is highly abundant and has been studied extensively in this region. Larval development of *B. bicaudatus* has been shown to be related to stream temperatures (Harper and Peckarsky 2006). During summer 2008, I collected mayflies with black wing-pads (BWP) (life stage IV) weekly for 5 weeks (8 July - 5 August) in both up and downstream reaches at 10 sites. BWP stage *B. bicaudatus* is within 24 hours of emerging from their aquatic habitat, has stopped eating (has empty guts) and therefore growing, and females have achieved full fecundity (Cowan and Peckarsky 1990; Peckarsky et al. 2001). Therefore, this life stage has been affected by its aquatic habitat as much as possible and represents the complete potential for aquatic environment influence on fitness.

I collected BWP mayflies with a D-net using 90 second kick samples. Samples were sorted for BWP *B. bicaudatus* in the field and preserved in 70% ethanol. In the lab, head capsule width (HCW) measurements and sex determinations were made using a dissecting scope at 25x magnification and an ocular micrometer. I converted HCW to dry masses (DM) using the following regression equations: female $DM = 1.5845 \times HCW^{3.8302}$ ($R^2 = 0.9343$, $n = 448$) and male $DM = 0.8237 \times HCW^{3.1808}$ ($R^2 = 0.9283$, $n = 399$). Those equations were derived from methods reported by Peckarsky *et al.* (2001) for estimating the relationship between HCW and DM for *Baetis*.

I calculated mean DM of female and male *B. bicaudatus* in both up- and downstream reaches at each site. I used the ratio of downstream DM/upstream DM rather than the differences to standardize for regional variation in body size among sites. Ratios greater than one indicated sites where mayflies matured at larger sizes downstream of beaver ponds. I used simple linear regression to test whether beaver pond morphology predicted upstream to downstream changes in body size for both male and female *B. bicaudatus*.

Timing of emergence of Baetis bicaudatus

In summer 2008, I also compared timing of emergence of *B. bicaudatus* upstream and downstream of beaver ponds by evaluating abundance curves of BWP individuals at up- and downstream reaches from weekly benthic samples. Since BWP larvae emerge within 24 hours, they are a good alternative to using emergence traps for collecting emerging *B. bicaudatus* (Peckarsky et al. 2001).

I implemented an analysis using two-sample Kolmogorov-Smirnov two-sided tests conducted in R (Harper and Peckarsky 2006; R Development Core Team 2008) to compare up and downstream emergence timing. I used the test statistic (D) as an index of the differences in timing of emergence. The test statistic was then assigned a positive or negative sign (positive if downstream emergence was accelerated compared to upstream emergence, as illustrated in cumulative distribution frequency plots, and negative if downstream emergence was delayed). Simple linear regressions were also used to test whether pond morphology predicted the timing of emergence (range of D values) of *Baetis*

larvae (females and males separately). With only 5 sampling dates for BWP *Baetis*, a spline interpolation curve was fit for each site increasing the number of data points from 5 to 10 so that the Kolmogorov-Smirnov tests could be implemented. Such artificial inflation of the degrees of freedom is of less concern because I was not basing conclusions on significance tests in this analysis, but rather used the relative test statistic values to examine associations with pond morphology.

Mechanisms explaining Baetis bicaudatus size variation

I used multiple linear regression to identify possible mechanisms explaining observed relationships between beaver pond morphology and changes in *B. bicaudatus* size at maturation. I tested variables (plecopteran (stonefly) predators, algal resources and stream temperature) evaluated by previous work to explain variation in *Baetis* size at metamorphosis (Peckarsky et al. 2001). Given that I did not record stream temperatures throughout the complete development time of *B. bicaudatus*, I used pond morphology as a proxy for temperature change in the multiple regressions because of its observed effect on stream temperatures. Abundances of plecopteran predators were obtained from benthic samples and benthic algae biomass (chlorophyll *a*) was estimated from rocks collected once during summer 2008 (see Chapter 2 for detailed methods). I used absolute *Baetis* size data from downstream reaches as the dependent variable for these tests of mechanisms rather than ratios of upstream vs. downstream sizes. Similarly, independent variables (predators, algal biomass and pond morphology ratio) predicting *Baetis* size were obtained from data collected from the downstream reach.

For the multiple linear regressions, a best subset analysis (using Bayesian Information Criterion as the model selection criterion) was applied to the three predictor variables and an intercept (no interaction terms) to determine which combination of variables did the best predicting female and male *B. bicaudatus* size at maturity downstream of beaver ponds. All analyses were conducted in R (R Development Core Team 2008).

Results

Baseflow temperature and pond morphology

Hydrologic conditions in this region were very different between 2007 and 2008 (Fig. 3), which was reflected in differences in the annual hydrographs and in baseflow water temperatures. Mean baseflow stream water temperatures for 2007, a low flow year, ranged from 10.4 - 14.3 °C in upstream reaches and 10.1 - 14.2 °C in downstream reaches (N = 12) (Table 1). In 2008, a year of very high snow pack, protracted period of thaw and extended high water, mean baseflow water temperatures were much colder, ranging from 6.7 – 10.0 °C in upstream reaches and 6.7 - 10.4 °C in downstream reaches (N = 10). Morphology ratios ($\ln(\text{hydraulic height (m)}/\text{pond surface area (ha)})$) of beaver ponds studied in 2007 ranged from 0.9 – 3.3 and from 1.5 – 4.2 for ponds studied in 2008 (Table 1). Despite dramatic differences in hydrology the regressions between pond morphology and changes in mean baseflow water temperatures between upstream and downstream reaches were significant and negative in both years (2007: slope = -0.16, $r^2 = 0.37$, $F_{1,10} = 5.91$, $P = 0.035$; 2008: slope = -0.17, $r^2 = 0.42$, $F_{1,8} = 5.78$, $P = 0.043$) (Fig. 4). Ponds with high morphology ratios (small

surface area ponds with high-head dams) generally had downstream cooling compared to upstream reference reaches and sites with low-head dams and large surface areas (low morphology ratios) experienced downstream warming.

Mayfly size and pond morphology

In summer 2008, mean dry mass (DM) of BWP male *B. bicaudatus* ranged from 1.15 - 1.57 mg in upstream reaches and from 1.18 - 1.53 mg in downstream reaches (Table 2). Dry mass of female BWP *B. bicaudatus* ranged from 1.43 - 2.28 mg in upstream reaches and 1.51 - 2.48 mg in downstream reaches. Pond morphology significantly predicted DM ratios of BWP *Baetis bicaudatus* females (downstream DM/upstream DM) (slope = 0.0096, $r^2 = 0.45$, $F_{1,7} = 5.72$, $P = 0.048$) with a positive regression coefficient (0.01) (Fig. 5). The ponds with high-head dams and smaller surface area produced larger female *B. bicaudatus* downstream than upstream. However, pond morphology did not significantly predict male DM ratios (slope = 0.0055, $r^2 = 0.16$, $F_{1,7} = 1.30$, $P = 0.3$), although the pattern of variation in male *Baetis* size was similar to that of females (Fig. 5).

Emergence timing and pond morphology

Pond morphology did not significantly predict differences between timing of emergence of *B. bicaudatus* in reaches upstream compared to downstream of beaver ponds during summer 2008 (females: slope = -0.13, $r^2 = 0.08$, $F_{1,8} = 0.73$, $P = 0.4$; males: slope = 0.17, $r^2 = 0.14$, $F_{1,8} = 1.30$, $P = 0.3$).

Potential mechanisms explaining relationships between pond morphology and mayfly size

I used multiple linear regressions to evaluate the influence of stonefly predators, food resources (benthic algal biomass) and pond morphology (a surrogate for stream temperature) on the absolute dry mass of male and female BWP *Baetis* downstream of beaver ponds. Evaluation of the full model (all three predictor variables and an intercept term) showed no significant predictor variables and did not predict a significant amount of variation in absolute female size ($F_{3,6} = 1.77$, $P = 0.3$) (Table 3). The full model for male *B. bicaudatus* also did not predict a significant amount of the variation in absolute size ($F_{3,6} = 4.10$, $P = 0.07$), but did reveal significant effects of algae and pond morphology on male size. The full models explained 20% and 51% of the variation in absolute dry mass of BWP female and male *B. bicaudatus* size, respectively. A best subsets analysis of the full multiple linear regression models (female and male separately) resulted in a reduced model leaving out stonefly predators as a predictor variable in both sexes (Table 3). The reduced models for both sexes indicated that pond morphology was a significant predictor, but the algae parameter was only significant for males (Table 3). The reduced male model significantly predicted the dry weight of mature male *B. bicaudatus* ($F_{2,7} = 6.72$, $P = 0.02$) and explained 56% of the variation. The female reduced model did not significantly predict the dry weight of mature female *B. bicaudatus* ($F_{2,7} = 3.08$, $P = 0.1$) and explained only 32% of the variation. Despite only one model significantly predicting size variation, pond morphology appeared to be the best of the three independent variables.

Discussion

The results of this study suggest that beaver ponds predictably influence their downstream reaches, but those effects depend on pond size and shape. Ponds with small surface areas and high-head dams cool the baseflow temperatures of their downstream reaches resulting in *B. bicaudatus* that mature at relatively larger sizes than their counterparts in upstream reference reaches. In contrast, large surface area ponds with low-head dams warm the baseflow temperatures of downstream reaches where mayflies emerge at sizes relatively smaller than in reference reaches upstream of ponds. While those patterns are intriguing, data obtained from these stream reaches were not sufficient to distinguish potential mechanisms explaining the effects of beaver pond morphology on observed differences in *B. bicaudatus* size at maturity even though some of the variables tested explained variation in *Baetis* size in an adjacent watershed (Harper and Peckarsky 2006; Peckarsky et al. 1993; Peckarsky et al. 2001).

Beaver ponds clearly cause changes in hydrology readily observed in groundwater flow paths (Lowry and Beschta 1994; Westbrook et al. 2006; White 1990), which are important determinants of stream water temperature regimes (Cadbury et al. 2008). Previous studies mapping groundwater flow paths around beaver dams provide a plausible explanation for the effects of beaver pond morphology on mayfly development that deserves further exploration. Beaver ponds also alter stream bed hydraulic conductivity independently of pond morphology, which increases the potential for upwelling downstream of beaver dams (Genereux et al. 2008). Those hydrologic and physical alterations support the groundwater –

surface water interaction hypothesized in this study and potentially explain why I observed cooling downstream of high-head dams and warming downstream of low-head dams during baseflow conditions in two years with very different hydrologic conditions (low and high water years) (Fig. 3).

The temperature patterns revealed in this study could also offer suggestions for managers regarding beaver dam removals for the purpose of creating better trout habitat. Beaver dam removals have been used as a common management practice designed to increase the interaction between groundwater and surface water with the ultimate goal of creating cold trout streams (McRae and Edwards 1994). However, our study provides evidence that destroying high-head dams could be counterproductive by actually decreasing the interaction between groundwater and surface water and thereby warming downstream reaches. Simple pond morphology measurements of the beaver ponds within trout habitat restoration projects could enable stream managers to optimize stream cooling by removing ponds systematically rather than removing all ponds within a river valley.

This study also has interesting implications with regard to the impacts of beaver impoundments on the fitness of stream insects. I observed a significant increase in size of mature female *B. bicaudatus* downstream of high-head ponds. Given that large *B. bicaudatus* females are more fecund (Peckarsky et al. 1993) and that I can predict effects on size of female *B. bicaudatus* from beaver pond morphology, I can also use patterns of beaver pond prevalence and morphology to predict local variation in mean individual fitness for *B. bicaudatus* females. It would then be possible to model the spatial variation of individual

fitness of *B. bicaudatus* females for a given population from known pond morphology for a catchment. This approach could also be used to compare populations in neighboring catchments and potentially explain some of the regional variation in mayfly size and fecundity.

Effects of pond morphology on male *B. bicaudatus* size differences upstream versus downstream of ponds in this study were not significant, but did follow a trend similar to that of females. The lack of a significant relationship to pond morphology could be a result of differences between male and female growth and development which is common in other insect species (De Block and Stoks 2003; Wiklund et al. 1991). One important difference between male and female *B. bicaudatus* fitness optimization is that males do not experience a large size advantage (Peckarsky et al. 2002). Instead, the probability of mating is highest for intermediate sized male *B. bicaudatus*. Similarly, differences in fitness optimization between males and females has been shown to result in different growth rates when exposed to similar environmental conditions in some species with sexual size dimorphism (De Block and Stoks 2003; Wiklund et al. 1991). Thus, differences between the responses of males and females associated with beaver pond morphology might be an example of environmental canalization, where environmental changes are identical for both sexes, but males exhibit different growth patterns than females because they optimize their fitness at an intermediate size while females optimize at larger sizes.

The timing of emergence of aquatic insects has been shown to vary predictably with environmental variables (Christman and Voshell 1992; Harper and Peckarsky 2006;

Peckarsky et al. 2001). For example, Harper & Peckarsky (2006) demonstrated experimentally that *B. bicaudatus* reared under higher temperature regimes (~2 °C on average) emerge earlier and at smaller sizes than those that have a longer development period. In this study I did not observe significant differences in the timing of emergence between adjacent stream reaches upstream and downstream of beaver ponds despite the predictable effects of pond morphology on stream water temperatures during baseflow. While it is possible that such temperature differences are too small to cause phenological shifts in mayflies, I cannot rule out the possibility that weekly sampling was not frequent enough to capture more subtle differences in peak emergence times between stream reaches upstream and downstream of beaver ponds. Emergence timing differences of more than a few days are biologically and ecologically significant for *B. bicaudatus* because males live as adults for a maximum of four days and females even fewer (Peckarsky et al. 2002; Vance 1996). Furthermore, I would need to obtain water temperature data over the entire development period of *B. bicaudatus* to test the relationship between growing degree days and development time directly.

It is also possible that the water temperatures during baseflow are not the primary mechanism driving the change in size of *B. bicaudatus* in this study. Beaver dams with greater upwelling associated with their morphology might function similarly to hypolimnetic release dams which experience cooler summer water temperatures (observed at baseflow in this study) and then winter warming (Ward and Stanford 1979). In a study where an impoundment increased the influence of groundwater and therefore warmed winter water temperatures, an increase in invertebrate growth was observed during the winter months (Fjellheim and

Raddum 2008). A similar mechanism might be working in this system where beaver ponds with summer baseflow cooling are having a warming effect during the winter, which could promote faster growth prior to entering the developmental period in late spring. Therefore, the size divergence of *B. bicaudatus* in upstream and downstream reaches might be occurring during the winter as a result of growth differences rather than during the summer as a difference in development rate.

In summary, the results of this study are consistent with the hypothesis that the effects of beaver ponds on the life histories of *Baetis* mayflies developing in their tail waters can be predicted by simple pond morphology characteristics. Temperature variability in the downstream reaches of beaver ponds is probably a result of the modification of groundwater – surface water interactions by beaver ponds, but further empirical verification of this mechanism is necessary. Additionally, morphological variation among beaver ponds may explain spatial variation within stream catchments of individual mayfly fitness and subsequent population growth. I hypothesize that observed effects of beaver ponds on mayfly fitness may be a function of temperature alterations as a result of groundwater – surface water interactions caused by beaver ponds.

Finally, predictable patterns of variation among beaver ponds could enable forecasting of downstream impacts on populations, communities and ecosystems in tail waters. As beaver populations continue to increase across North America and rapidly invade South America, understanding and predicting those alterations to the ecosystem will be vital. Given that up to 40% of the length of streams in a catchment can be occupied by beavers (Hammerson

1994), they are clearly a common geomorphic agent in streams that cannot be ignored in the landscape and should be incorporated into stream ecology theory.

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Table 1 Pond site elevation, morphology characteristics and mean baseflow stream temperatures for reaches up and downstream of beaver ponds studied in 2007 and 2008. WBC indicates sites on West Brush Creek; CC indicates sites on Coal Creek; EBC indicates sites on East Brush Creek; OBJ indicates sites on Oh-Be-Joyful Creek; CMC indicates sites on Cement Creek.

Site	Year	Site Elevation (m)	Hydraulic Height (m)	Pond Length (m)	Max Pond Width (m)	Surface Area (ha)	Pond morphology ratio	Mean Temperature (°C)	
								Up	Down
WBC1	2007	2911	1.77	26.9	39.8	0.074	3.2	10.7	10.7
WBC2	2007	2930	1.00	32.0	22.9	0.036	3.3	10.5	10.1
WBC4	2007	2924	0.75	26.6	31.3	0.046	2.8	10.4	10.3
WBC5	2007	2896	0.50	34.7	48.0	0.091	1.7	12.0	12.0
CC1	2007	2889	0.91	52.9	28.2	0.093	2.3	10.9	11.3
CC2	2007	2945	0.82	20.2	15.4	0.036	3.1	14.3	14.2
EBC1	2007	2847	1.00	53.5	88.0	0.187	1.7	11.1	11.5
EBC3	2007	2836	0.34	71.8	23.9	0.104	1.2	11.5	11.6
EBC4	2007	2836	0.28	21.7	16.9	0.031	2.2	11.8	11.7
OBJ1	2007	2911	1.23	47.7	57.6	0.182	1.9	13.7	13.7
OBJ2	2007	2944	1.19	91.0	116.6	0.497	0.9	13.6	13.8
OBJ3	2007	2955	1.22	49.9	63.0	0.144	2.1	12.1	12.3
WBC1	2008	2911	1.20	26.6	36.2	0.047	3.2	9.1	9.2
WBC2	2008	2930	0.75	19.8	7.6	0.0125	4.1	9.1	8.8
WBC4	2008	2924	0.81	33.9	11.5	0.013	4.1	8.9	8.7
WBC5	2008	2896	0.76	29.5	48.4	0.162	1.5	10.0	10.4
CMC1	2008	2893	0.46	30.7	10.3	0.025	2.9	8.7	8.7
CMC2	2008	2958	0.58	45.8	19.9	0.064	2.2	8.5	8.7
CMC3	2008	2994	0.42	23.1	19.1	0.031	2.6	8.7	8.6
CMC4	2008	3116	0.83	14.5	13.0	0.014	4.1	7.0	6.8
CMC5	2008	3120	2.43	48.6	10.1	0.037	4.2	6.7	6.9
CMC6	2008	3130	0.87	19.0	19.5	0.026	3.5	7.0	6.7

Table 2 Mean dry mass and sample sizes for female and male black wing-pad *Baetis bicaudatus* collected in reaches up and downstream of beaver ponds in 2008. Site codes are the same as in Table 1. Values in parentheses were extreme outliers (high Cook's Distance values) and, therefore, not included in regression analyses (see Fig. 5).

Site	Mean Dry Mass (mg)				Sample sizes			
	Upstream		Downstream		Upstream		Downstream	
	Female	Male	Female	Male	Female	Male	Female	Male
WBC1	1.97	1.39	1.83	1.37	23	28	41	30
WBC2	1.43	1.15	1.51	1.18	6	15	3	2
WBC4	1.55	1.19	1.67	1.23	30	35	28	16
WBC5	2.27	1.53	2.15	1.51	59	56	60	59
CMC1	2.12	1.39	2.07	1.33	43	51	44	22
CMC2	(2.02)	(1.36)	(2.48)	(1.44)	54	43	9	14
CMC3	1.79	1.34	1.76	1.31	79	75	127	106
CMC4	2.10	1.53	2.14	1.49	19	16	38	18
CMC5	2.14	1.49	2.10	1.53	35	24	19	16
CMC6	2.05	1.57	2.09	1.45	35	21	44	24

Table 3 Multiple regression explaining variation of *Baetis bicaudatus* males and females that matured downstream of beaver dams. Coefficients and P-values in bold indicate significant predictors.

Model Type	Sex	Adj R ²	df	F-value	Parameter	Coefficient	P-value
Full	Female	0.20	3,6	1.77	Intercept	1.987	<0.001
					Algae	0.072	0.180
					Stonefly	0.010	0.911
					Pond Morphology	-0.009	0.077
	Male	0.51	3,6	4.10	Intercept	1.307	<0.001
					Algae	0.04	0.037
					Stonefly	0.042	0.622
					Pond Morphology	-0.003	0.052
Best Subsets Selected	Female	0.32	2,7	3.08	Intercept	1.996	<0.001
					Algae	0.075	0.090
					Pond Morphology	-0.009	0.055
	Male ^a	0.56	2,7	6.72	Intercept	1.319	<0.001
					Algae	0.046	0.009
					Pond Morphology	-0.003	0.040

^a indicates model significantly predicts *Baetis bicaudatus* size ($P \leq 0.05$)

Figure Headings

Fig. 1 Stereotypical study site and pond measurements for principle components analysis evaluating pond shape. *Gray fill* indicates water surface and *brick fill* indicates beaver dam. Pond measurements indicated by double headed arrows are labeled as follows: W – max width, L – pond length and H – hydraulic height. Dashed lines indicate pond surface area (SA).

Fig. 2 Principal components analysis biplot of two major components. See Fig. 1 for arrow letter codes and Table 1 for site codes.

Fig. 3 Discharge from USGS gaging station (09112200) on the East River downstream of the confluence of Cement Creek in 2007, 2008 and a 15 year average (data begin 1 May and end 31 August). Dashed line at $7 \text{ m}^3/\text{s}$ indicates approximate baseflow conditions at the station and can be used to infer the timing of baseflow conditions in tributaries of the East River. Dots on 2007 and 2008 hydrographs indicate the point in the hydrograph when baseflow temperatures began and squares indicate hydrograph on nutrient sampling dates.

Fig. 4 The relationship between beaver pond morphology and the arithmetic differences in mean base flow temperatures between reaches downstream and upstream of beaver ponds. The Y-axis represents mean downstream minus mean upstream temperatures so that positive numbers indicate sites where beaver ponds warm the downstream

reaches. Both 2007 (*solid black line*) and 2008 (*dashed line*) pond morphology significantly predicted temperature changes.

Fig. 5 Relationship between beaver pond morphology and the ratio of mean dry weights of male and female *B. bicaudatus* in reaches downstream compared to reaches upstream of beaver ponds. *B. bicaudatus* ratios > 1 indicate sites where mayflies matured at larger sizes downstream of beaver ponds. A significant regression was observed for females (*solid black line*), but not for males. Labeled sites were not included in the regression analysis as a result of high Cook's Distance values suggesting high leverage and therefore outlier status.

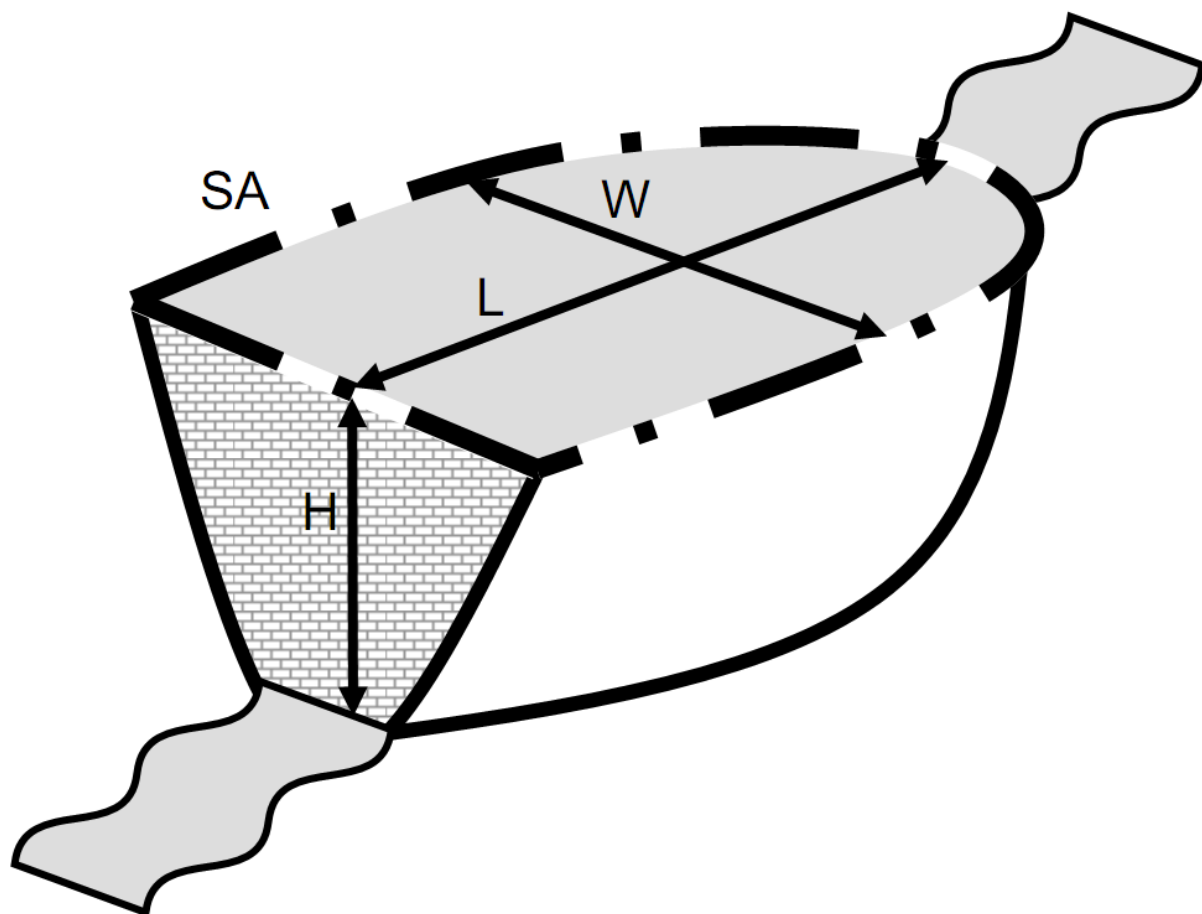
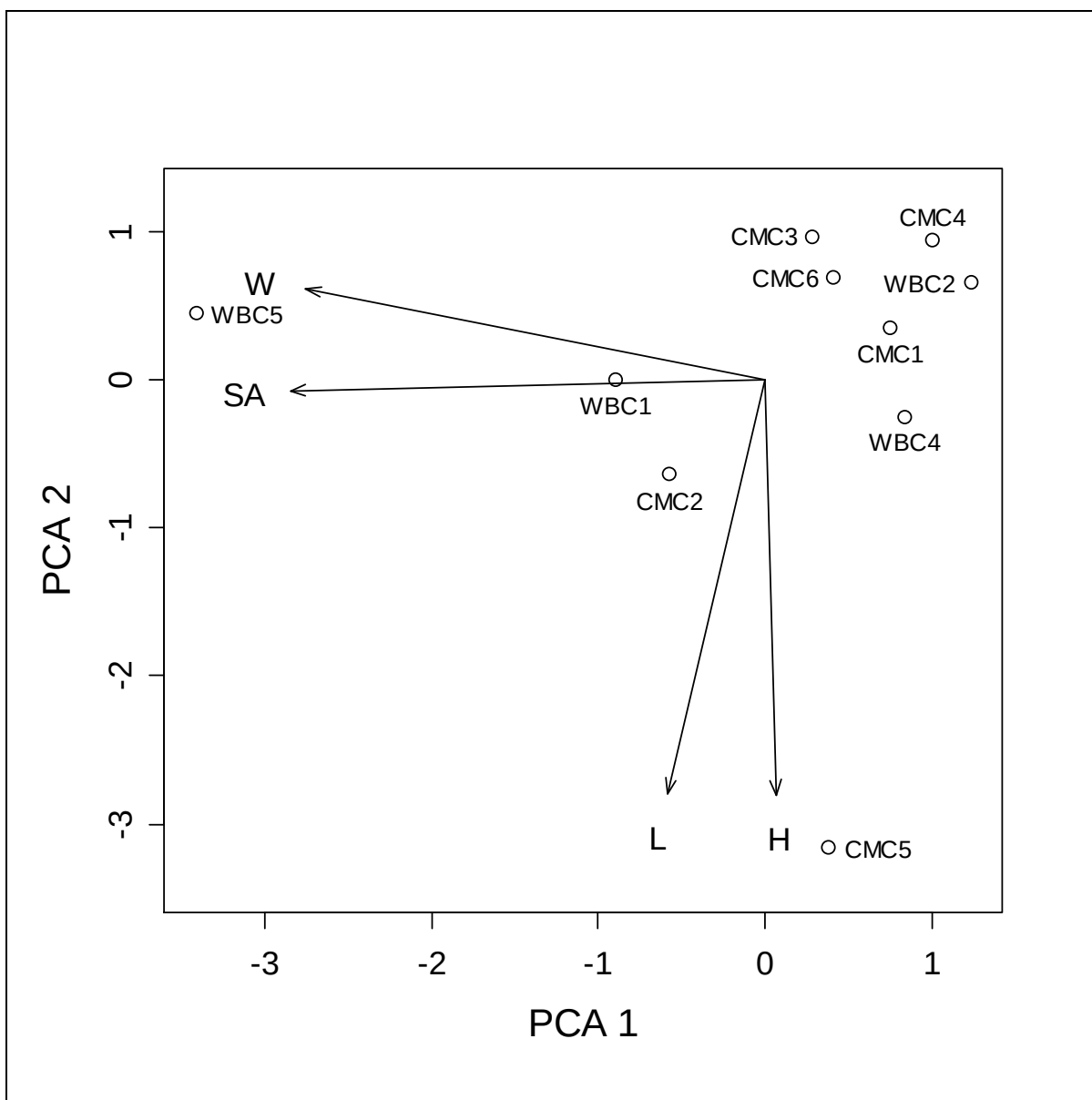
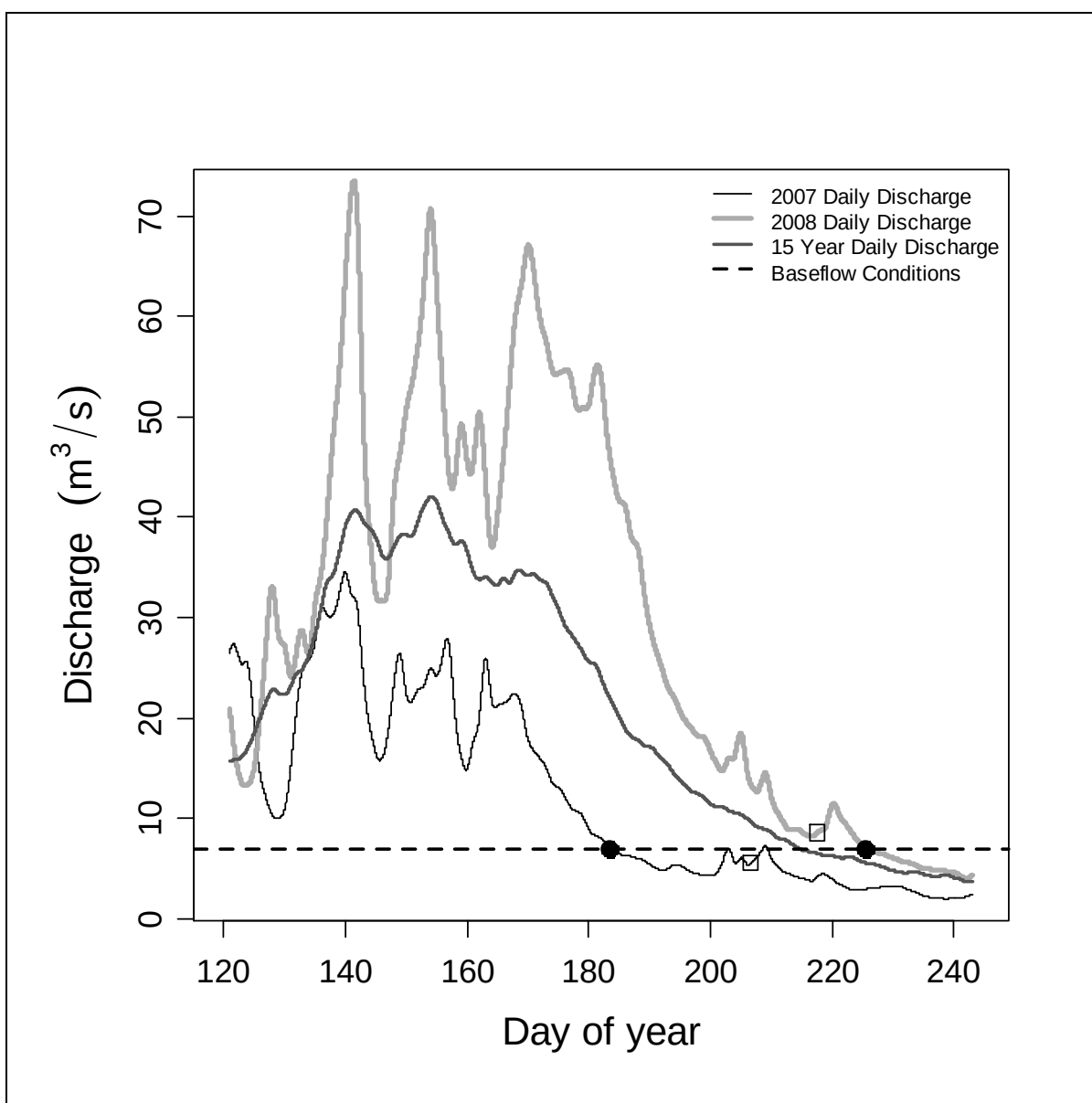


Fig. 1

**Fig. 2**

**Fig. 3**

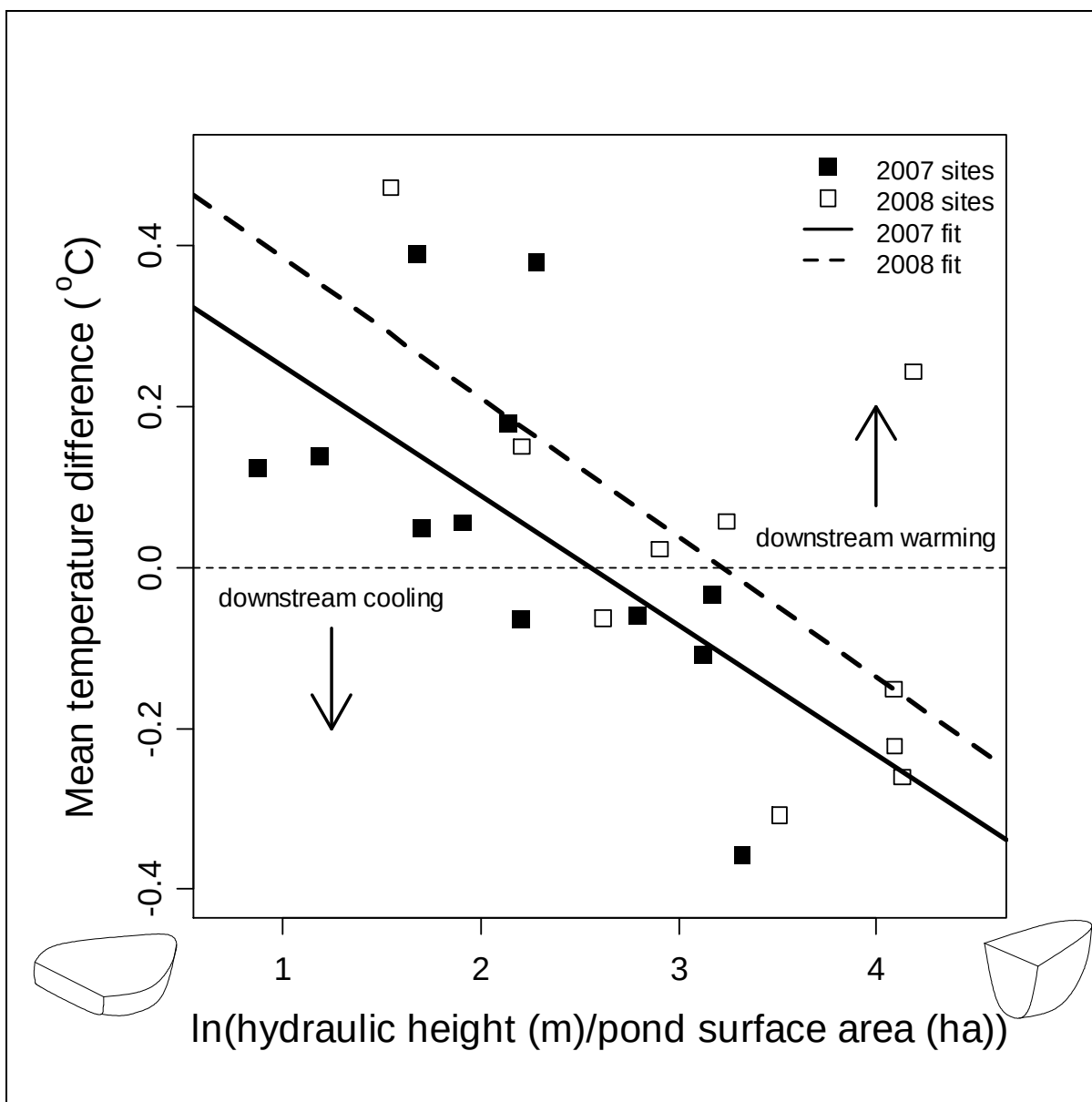


Fig. 4

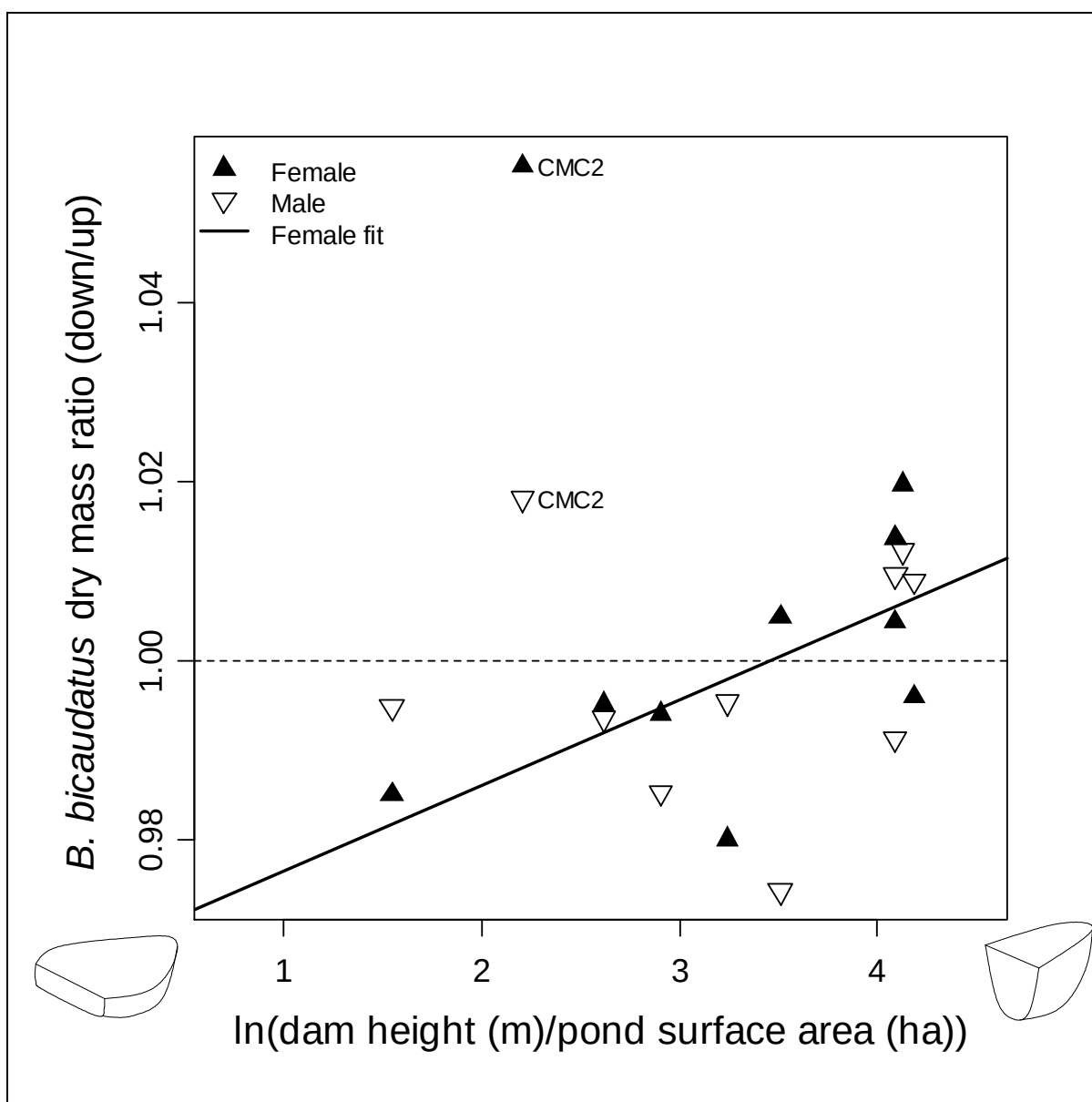


Fig. 5

Chapter 2

Does the morphology of beaver ponds alter food webs of downstream reaches?

Abstract

Differences among lake sizes and shapes have been used to explain variation in biological, chemical and physical characteristics of lentic systems. Although beaver ponds also show a variety of sizes and shapes, previous studies have not similarly examined the downstream effects of such variation on stream food webs. This study evaluated downstream effects of multiple beaver ponds in five catchments over two years (12 ponds in 2007 and 10 ponds in 2008) in the Colorado Rockies near the Rocky Mountain Biological Laboratory. Pond morphology was measured as the natural log transformed ratio of beaver dam height to pond surface area and related to pond spillover phytoplankton and characteristics of the food webs downstream including: nutrient concentrations, limiting nutrients, benthic algae, benthic organic matter, and benthic invertebrate consumers. Nitrate concentration increased consistently downstream of beaver ponds, but only in summer 2007. In contrast, soluble reactive phosphorus concentration increased downstream of small surface area ponds with high hydraulic head dams in 2007, but not in 2008. I speculate that effects were detected in 2007 because groundwater influences predominate during low-flow years (2007); and that

surface runoff mask the effects of groundwater during the high-flow years (2008). There was no single limiting nutrient within or among catchments, and limiting nutrients did not vary with pond morphology or change systematically from upstream to downstream of beaver ponds which suggests that beaver activity does not predictably affect limiting nutrients. Although benthic algal biomass and benthic organic matter decreased downstream of high-head beaver dams compared to reference reaches upstream, the abundances of the invertebrate consumers that use those resources (grazers and detritus-feeders) were not predicted by pond morphology. In contrast, suspension feeding invertebrates increased downstream from beaver ponds with high-head dams and small surface area. This effect could not be explained by variation in the chlorophyll *a* in water spilling over beaver dams. I conclude that beaver ponds do not have consistent effects on downstream food webs and that the effects of variation in pond morphology on available phosphorus, algal and benthic organic matter resources downstream of beaver dams may depend on seasonal hydrologic conditions.

Introduction

The ability of the North American beaver (*Castor canadensis*) to alter their environment has been appreciated by hydrologists, geomorphologists and ecologists for decades (Collen and Gibson 2001). Beaver ponds were once ubiquitous across North American lotic systems and are currently returning to pre-European settlement densities (Cunningham et al. 2006; Foster et al. 2002; Naiman et al. 1988). Predicting the location of beaver ponds in watersheds has been evaluated from a beaver food-resource perspective as well as a geomorphology

perspective (Dieter and McCabe 1989; Jakes et al. 2007). Results from those studies suggest that beaver 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 and Stanford 1983). Therefore, understanding the influence of those structures embedded in otherwise continuous stream networks is vital for understanding the fundamentals of longitudinal stream processes.

In addition to the potential of beaver ponds to disrupt lotic stream habitats, there is also enormous variability among the lentic habitats created by beaver. Beaver ponds vary dramatically 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 and Wittgren 1994; Arheimer and Wittgren 2002; Koskiahio 2003; Reinhardt et al. 2005; Tonderski et al. 2005). Results from those wetland systems provide a 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 (Correll et al. 2000; Devito and Dillon 1993; Margolis et al. 2001a), periphyton (Coleman and Dahm 1990), and sedimentation (Butler and Malanson 1995), only site-specific mechanisms have been offered to explain the variation observed downstream among studies.

If beaver ponds alter stream water nutrients and/or benthic organic matter transport in bottom-up controlled trophic systems, 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 (Clifford et al. 1993; Margolis et al. 2001b; McDowell and Naiman 1986; Smith et al. 1991) often report inconsistent effects. For example, studies have reported greater numbers of invertebrate suspension feeders downstream of beaver ponds (Clifford et al. 1993; Margolis et al. 2001b), no significant changes in suspension feeder abundance (McDowell and Naiman 1986), or decreased abundance downstream (Smith et al. 1991). Studies are needed to identify factors explaining the variation among observed effects of beaver ponds on downstream food webs.

The goals of this study were to evaluate whether alterations of lotic habitats downstream of beaver ponds (relative to upstream reference sites) were consistent among beaver ponds, or if beaver pond morphology could explain the variation in downstream food webs. I hypothesized that ponds with high-head dams and small surface areas would have higher nutrient concentrations due to greater groundwater upwelling into the downstream reach. Additionally, I tested for relationships between pond morphology and downstream nutrient limitation, benthic algae, benthic organic matter and pond spill-over phytoplankton as potential resources for invertebrate consumers. Finally, I tested effects of beaver ponds in general and pond morphology in specific on invertebrate consumers downstream.

Methods

Study Sites

Study sites were located near the Rocky Mountain Biological Laboratory on the western slope of the Colorado Rockies near Crested Butte, Colorado, USA. Twelve beaver ponds were studied in summer 2007 from 4 catchments (Coal Creek (2), East Brush Creek (3), Oh-Be-Joyful Creek (3) and West Brush Creek (4)), and 10 beaver ponds in summer 2008 from two catchments (Cement Creek (6) and West Brush Creek (4)) (Fig. 1). The four West Brush Creek sites were used in both 2007 and 2008. Each site consisted of a specific geomorphic pattern: an upstream lotic reach, lentic pond and downstream lotic reach (See Fig. 1 in Chapter 1). 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 and Waddington 1990). Since the stream reach between Cement Creek 4 (CMC4) and Cement Creek 5 (CMC5) was relatively short (50 m) the downstream reach of CMC5 was used as the reference reach of CMC4 for some parameters (benthic invertebrates and benthic organic matter). Ponds were arrayed along an axis of dam height/pond area ratios ($\ln(x)$ transformed), with smaller ratios indicating low-head, large surface area ponds and higher ratios being high-head, small surface area ponds. (See Chapter 1 for specific site characteristics and detailed methods for measuring pond morphology.)

Stream water nutrient concentrations

Stream water samples were collected once each summer from 24-29 July 2007 and 4-5 August 2008 to estimate nutrient concentrations upstream and downstream of each pond as

well as the primary pond spillover. Samples were taken at baseflow (approximately three weeks after baseflow conditions had been reached) in 2007, but during the tail end of the descending limb of the annual hydrograph in 2008 because of high water and late snowmelt conditions that year (See Fig. 3 in Chapter 1). Samples were filtered in the field using a 60 ml syringe and filter housing (Whatman glass microfiber filters with pore size of 0.7 μm). Soluble reactive phosphorus (SRP), nitrate and ammonium samples were frozen for future 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-NH₃H) and nitrate via the Automated Cadmium Reduction Method (4500-NO₃-F) (Franson 1985). SRP samples were analyzed on a spectrophotometer via the Ascorbic Acid Method (4500-P E). Limitation of detection (LOD) for ammonium sample processing was 3 $\mu\text{g/L}$ and nitrate LOD was 2 $\mu\text{g/L}$ on the Astoria Pacific analyzer. LOD for SRP on the spectrophotometer was 0.5 $\mu\text{g/L}$. Concentrations below the LOD for these analytes were assigned half the LOD concentration (ammonium – 1.5 $\mu\text{g/L}$; nitrate – 1 $\mu\text{g/L}$; SRP – 0.25 $\mu\text{g/L}$).

To evaluate the change in nutrient concentrations associated with beaver ponds, the ratio of the downstream concentration to the upstream concentration was calculated. Ratios of response variables were used 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 of each pond. Nutrient ratios of upstream/spillover concentrations and spillover/downstream concentrations were also compared to evaluate the potential for pond spillover nutrients to augment or dilute downstream nutrient inputs from

groundwater. Those additional ratio evaluations were only conducted when there were significant changes from upstream to downstream reaches.

Nutrient limitation

Nutrient diffusing substrates (NDS) were deployed upstream and downstream at 10 sites in 2008 to test whether nutrient limitation was affected by beaver ponds (Tank and 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 and Dodds 2003).

To determine if the overall magnitude of nutrient limitation was different upstream and downstream of beaver ponds in general, 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 reach response ratios. A positive response ratio difference indicates more

nutrient limitation downstream and a negative response ratio difference indicates less nutrient limitation downstream.

Benthic and pond spillover algae biomass

Biomass of benthic algae in the upstream and downstream reaches was estimated to determine if food resources for grazing invertebrates were altered by beaver ponds. 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 and Collins 1997). Extracted rocks were traced on paper and the paper cutouts were scanned with a LI-COR LI-3100C area meter (0.1 mm² resolution and an accuracy of $\pm 1\%$) to estimate a two-dimensional area of stream bed occupied by each rock. Rock areas ranged from ~15 - 65 cm². Rock areas were used to calculate a mean algal biomass per unit area (mg chlorophyll *a* /m²) 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 one liter of pond spillover water through a Whatman glass microfiber filter with a pore size of 0.7 μm . Filters were frozen and later extracted and analyzed fluorometrically by methods described above for the benthic algae samples. Spillover chlorophyll *a* concentrations were transformed ($\ln(x)$) to meet normality assumptions.

Benthic organic matter

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 bucket was used to isolate a known area of stream bottom (0.05m^2) and then suspend the BOM into the water by gently disturbing the substrate. The water in the bucket was then sub-sampled and filtered onto a pre-ashed and pre-weighed 47mm Whatman glass microfiber filter with a pore size of $0.7\mu\text{m}$. 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 hours 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 ($\text{g AFDM}/\text{m}^2$) 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-second kick sample that covered one complete transect of the stream. Samples were sorted in the field and preserved in 70% ethanol. Abundance was compared among sites as catch per unit effort (30 seconds).

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 the analysis due to high variability in functional feeding groups within the family. Preliminary benthic samples taken in summer 2007 indicated that Chironomidae occupied from 9-64% of the total community abundance in streams of this region. Chironomid abundance was on the low end of this range in the 2008 study streams because of high water and low population levels of the nuisance diatom, *Didymosphenia geminata* (unpublished observations).

Effects of beaver ponds on benthic invertebrate food webs were tested by calculating ratios of abundances for each FFG (downstream/upstream) and comparing them to pond morphology. Shredders and collector-gatherers were combined into one group (detritus-feeders) for analyses. FFG abundance ratios 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, evaluation of whether all beaver ponds have similar effects downstream was conducted using one-sample t-tests to determine if there were consistent increases or decreases in a parameter downstream of ponds compared to their upstream reaches. T-tests were conducted on the ratios of downstream/upstream measurements with a null hypothesis of $\mu = 1$ (or 0 if the ratio was log transformed to meet normality assumptions assessed by Lillifors tests for

normality). Rejection of the null hypothesis would suggest beaver ponds are consistently increasing or decreasing the measured variable downstream.

If the t-test failed to reject the null hypothesis, evaluation of whether beaver pond morphology was related to changes in each parameter was made using simple linear regression with the pond morphology ratio ($\ln(\text{dam height (m)}/\text{pond surface area(ha)})$) as the independent variable and the downstream/upstream parameter ratios the dependent variables. Downstream/upstream ratios >1 indicate that a variable increases downstream of the beaver pond and ratios <1 indicate a decrease in that variable downstream of the pond. For nutrient limitation response ratios, differences (downstream – upstream) were employed rather than ratios. Positive differences indicate increases in nutrient limitation downstream and negative values indicate decreases in nutrient limitation downstream.

In regression analyses, Cook's Distance values were used to identify data points as outliers (Cook's Distance greater than 0.5). Outliers were removed from all regression analyses and resulted in some variation in the number of degrees of freedom for various analyses. 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 soluble reactive phosphorus (SRP) had greater variability in 2007 than 2008 ranging from below detection limits (BDL) to 9.4 µg/l in the upstream reaches and from BDL to 11.5 µg/l in downstream reaches in 2007, and from BDL to 1.0 µg/l upstream and from BDL to 1.2 µg/l downstream in 2008 (Table 1). Similarly, nitrate achieved higher concentrations and had a greater range of concentrations in 2007 (upstream: 6.2 to 135.0 µg/l; downstream: 6.8 to 138.2 µg/l) versus 2008 (upstream: 5.1 to 80.2 µg/l; downstream: 4.7 to 85.2 µg/l) (Table 1). In contrast, ranges of ammonium concentrations were similar between 2007 (upstream: 4.0 to 8.1 µg/l; downstream: BDL to 9.6 µg/l) and 2008 (upstream: BDL to 20.9 µg/l; downstream: BDL to 6.6 µg/l).

There were no consistent increases or decreases in ammonium or SRP concentrations from upstream to downstream of beaver ponds in either year (4 t-tests; $P > 0.05$). However, nitrate concentrations (mean difference $\pm$ SE) in 2007 were significantly higher downstream of beaver ponds (2.76 ± 0.96 µg/l) (t-test, $t_{11} = 5.67$, $P = 0.0001$). Nitrate concentrations in 2008 did not differ upstream versus downstream of beaver ponds (t-test, $t_9 = 0.60$, $P = 0.6$).

Ammonium concentration ratios were not significantly related to pond morphology in 2007 or 2008 (2007 regression, slope = 0.18, $r^2 = 0.21$, $F_{1,10} = 2.59$, $P = 0.1$; 2008 regression, slope = -0.60, $r^2 = 0.17$, $F_{1,8} = 1.67$, $P = 0.2$). However, SRP ratios were significantly predicted by pond morphology in 2007 (regression, slope = 0.61, $r^2 = 0.49$, $F_{1,9} = 8.74$, $P = 0.02$), but not 2008 (regression, slope = -0.22, $r^2 = 0.16$, $F_{1,8} = 1.51$, $P = 0.3$) (Fig. 2).

Regressions of pond morphology and SRP ratios between upstream/spillover and spillover/downstream in 2007 were also not significant (up/spillover regression: slope = -

0.47, $r^2 = 0.28$, $F_{1,9} = 3.50$, $P = 0.09$; spillover/downstream regression: slope = -0.14, $r^2 = 0.04$, $F_{1,9} = 0.42$, $P = 0.5$).

Effects of beaver ponds on nutrient limitation

Nutrient diffusing substrates revealed high variability in the limiting nutrient among sites. In three of the 10 sites tested in 2008 there was no change 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 NDS substrates were covered by bed movement upstream.)

The mean phosphorus limitation response ratio difference was -0.11 with a 95% confidence interval spanning -0.27 to 0.05. The phosphorus limitation response ratio difference demonstrated no consistent effects of beaver ponds on phosphorus limitation (t-test, $t_8 = -1.55$, $P = 0.2$). Furthermore, pond morphology did not significantly predict phosphorus limitation response ratio differences (regression, slope = -0.046, $r^2 = 0.04$, $F_{1,7} = 0.29$, $P = 0.6$). Nitrogen limitation response ratio differences also did not demonstrate a consistent effect of beaver ponds on downstream nitrogen limitation (t-test, $t_8 = 0.48$, $P = 0.6$). Similar to phosphorus, beaver pond morphology did not significantly predict changes in nitrogen limitation downstream (regression, slope = -0.14, $r^2 = 0.03$, $F_{1,7} = 0.25$, $P = 0.6$).

Effects of beaver ponds on basal resources

One sample t-tests indicated that neither algal biomass nor BOM changed consistently from upstream to downstream of beaver ponds (algae: $t_8 = -1.80$, $P = 0.1$; BOM: $t_7 = 1.62$, $P = 0.1$). There was no significant relationship between pond morphology and the downstream/upstream ratio of benthic algal biomass in 2008 (regression, slope = -0.13 , $r^2 = 0.27$, $F_{1,7} = 2.53$, $P = 0.2$) (Fig. 3A). However, removal of one statistical outlier (Cement Creek Site 3) revealed a significant negative relationship between pond morphology and relative algal biomass (regression, slope = -0.16 , $r^2 = 0.49$, $F_{1,6} = 5.82$, $P = 0.05$) suggesting that algal biomass decreased downstream of high-head, small surface area ponds. Similarly, BOM AFDM decreased downstream of high-head ponds as indicated by a significant negative relationship between beaver pond morphology and BOM AFDM ratios (downstream BOM AFDM / upstream BOM AFDM) (regression, slope = -0.52 , $r^2 = 0.62$, $F_{1,6} = 9.71$, $P = 0.04$) (Fig. 3B). In contrast, pond spillover phytoplankton was not related to pond morphology (regression, slope = 0.055 , $r^2 = 0.01$, $F_{1,8} = 0.11$, $P = 0.8$) (Fig. 3C).

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 consistently between upstream and downstream of beaver dams (response ratios not significantly different from one (or $\ln(1+1)$ for suspension feeders who were $\ln(x+1)$ transformed) (suspension feeders: $t_8 = 2.08$, $P = 0.07$; grazers: $t_9 = -0.10$, $P = 0.9$; predators: $t_9 = 0.59$, $P = 0.6$; detritus feeders: $t_9 = 1.16$, $P = 0.3$). Furthermore, there were no significant regressions between pond morphology and the downstream/upstream ratios of grazers, predators or detritus feeders (grazers: slope = 0.10, $r^2 = 0.04$, $F_{1,8} = 0.31$, $P = 0.6$; predators: slope = 0.18, $r^2 = 0.03$, $F_{1,8} = 0.26$, $P = 0.6$; detritus feeders: slope = 0.26, $r^2 = 0.02$, $F_{1,8} = 0.17$, $P = 0.7$) (Fig. 3D, E). However, a positive relationship between pond morphology and the downstream/upstream ratio of suspension feeders (regression, slope = 0.76, $r^2 = 0.61$, $F_{1,7} = 10.92$, $P = 0.01$) suggested abundance of that FFG increased downstream of high-head, small surface area ponds (Fig. 3F).

Discussion

This study clearly demonstrates that beaver ponds have very few consistent effects on downstream food webs. Instead, the effects of beaver ponds on downstream nutrients, primary resources and invertebrate consumers were highly variable. For example, soluble reactive phosphorus (SRP) was the only nutrient that changed predictably with pond morphology, and only during a low water year and after baseflow conditions were reached. Beaver pond morphology did predict variation in the downstream abundance of some basal

resources (periphyton biomass and benthic organic matter), but not others (pond spillover chlorophyll *a*). Additionally, pond morphology affected the abundance of suspension-feeding benthic invertebrates, but not that of benthic periphyton grazers or benthic 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 indicating that the driving mechanisms for SRP retention and release in this study were likely controlled by either sorption on sediments and/or by microbial uptake (algae on pond sediments included).

Hydrology can drive SRP transport in some wetland systems (Reinhardt et al. 2005; Schulz and Herzog 2004). In fact, other studies have found extreme changes in discharge to result in nutrient sources becoming nutrient sinks (Stanley and Boulton 1995). The different relationships between SRP and pond morphology observed in 2007 and 2008 may be explained similarly by extreme differences in hydrology (See Fig. 3 in Chapter 1). 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 attained for more than three

weeks, but 2008 samples were collected before snowmelt flows had completely receded (See Fig. 3 in Chapter 1). Dilution of SRP was likely the result of the very low concentrations measured in 2008.

Nitrate concentrations in 2007 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 and Dahm 1990). Genereux et al. (2008) determined that stream substrate hydraulic conductivity increased downstream of beaver ponds. They hypothesized that increased hydraulic conductivity downstream of beaver ponds would result in the consistent transport of nitrate from the hyporheic zone to the surface waters. High water dilution of any groundwater nitrate inputs could explain why no systematic increase in nitrate concentration was observed downstream of beaver ponds 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.

The regression analyses suggested that the biomass of benthic algae was altered by pond morphology. 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 unaffected by pond morphology. Other potential mechanisms controlling algal biomass could be grazing invertebrates (Álvarez and Peckarsky 2005) and hydrologic scouring (Francoeur and Biggs 2006). However, there was no significant 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 and 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.

In two constructed wetlands, the size and shape of the wetland were important predictors of total suspended solid transport through the wetland (Koskiaho 2003). As expected, the

regression analyses showed a negative, however weak, relationship between pond morphology and benthic organic matter ash free dry mass. Standing stock of BOM was lower downstream of high-head dams (Fig. 3B) suggesting that ponds with higher dams, but smaller surface areas are more retentive of particulate organic matter than ponds with low dams and large surface areas. Similarly, human dams are reported to have predictable changes on BOM accumulation upstream of impoundments (Ward and Stanford 1983). Again, the extreme hydrologic conditions during the 2008 sampling period might have dampened the expected pattern because high flows often carry large loads of suspended organic matter (Francoeur and Biggs 2006). BOM samples were taken during the descending limb of spring snowmelt while discharge was still high and therefore more benthic organic matter than expected would be transported to downstream reaches of even high dams.

The only functional feeding group (FFG) whose abundance varied predictably with pond morphology was the suspension feeders. Overwhelming evidence from man-made reservoirs and lakes shows widespread increases in abundance of suspension feeders downstream of the reservoirs and in lake outlets (Mackay and Waters 1986; Richardson and Mackay 1991). Previous studies similarly documented increases in suspension feeding invertebrates downstream from beaver ponds (Clifford et al. 1993; Margolis et al. 2001b). 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 and Mackay 1991). Despite such evidence from other stream-pond-stream habitats, a consistent 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 and 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 and 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 and 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 and Biggs 2006) and alter abundance and richness of benthic invertebrates (Holomuzki and Biggs 1999; Wagner and 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. Therefore, effects observed in 2008 under high flow conditions are likely to be more evident during periods of low flow. A robust test of the influence of

variation in hydrologic regime on the downstream effects of beaver ponds requires more data from both low and high flow years.

In summary, this study suggests that variation in the effects of beaver ponds on some stream nutrients, benthic food 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 their downstream food webs. Beaver impound much smaller waterways than most human-constructed impoundments or natural lakes and therefore, only limited extrapolation from human impoundments and natural lake systems can be made to beaver ponds. A new conceptual framework is needed to describe the importance of beaver impoundments in streams and the landscape which occur at smaller temporal and spatial scales. That framework will need to take into consideration that beaver ponds do not cause consistent alterations in downstream food webs.

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Table 1 Summary of concentrations of soluble reactive phosphorus (SRP), ammonium (NH₄) and nitrate (NO₃) from each site. 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/correlation analyses (see Figure 2).

Site	Year	Pond morphology ratio	Analyte								
			SRP (µg/L)			NH ₄ (µg/L)			NO ₃ (µg/L)		
			Up	Spill	Down	Up	Spill	Down	Up	Spill	Down
WBC1	2007	3.2	0.7	0.9	0.5	7.4	6.6	6.0	135.0	137.6	138.2
WBC2	2007	3.3	0.8	0.6	0.3	5.3	5.7	6.0	96.8	100.8	103.5
WBC4	2007	2.8	0.7	0.3	0.6	5.0	4.5	5.7	121.4	128.3	134.2
WBC5	2007	1.7	0.7	1.2	3.2	7.4	7.1	6.5	126.5	128.2	127.2
CC1	2007	2.3	4.8	3.7	6.3	6.2	5.6	6.7	16.9	18.2	19.2
CC2	2007	3.1	11.5	9.2	9.4	9.4	8.1	7.5	11.5	11.7	12.7
EBC1	2007	1.7	(5.3)	(0.6)	(0.25)	9.6	6.8	8.0	15.4	15.7	15.9
EBC3	2007	1.2	0.3	0.5	0.5	6.7	8.6	8.1	24.9	30.5	25.7
EBC4	2007	2.2	0.3	0.3	0.5	6.9	6.5	6.4	29.5	30.7	30.4
OBJ1	2007	1.9	0.8	1.0	0.5	5.5	49.1	4.0	6.2	12.1	6.8
OBJ2	2007	0.9	0.6	0.3	1.0	1.5	6.5	7.3	7.2	7.6	7.7
OBJ3	2007	2.1	0.7	0.9	0.8	6.7	7.3	6.1	6.6	7.9	7.3
WBC1	2008	3.2	0.7	0.6	0.5	1.5	1.5	13.6	78.4	78.3	85.2
WBC2	2008	4.1	0.7	0.8	1.0	1.5	1.5	20.9	70.8	71.4	69.0
WBC4	2008	4.1	1.0	1.0	1.0	1.5	1.5	16.4	74.2	75.0	74.2
WBC5	2008	1.5	1.2	1.3	0.9	1.5	1.5	1.5	80.2	80.9	80.0
CMC1	2008	2.9	1.2	0.9	0.6	1.5	1.5	1.5	16.6	16.0	15.4
CMC2	2008	2.2	0.8	0.7	0.6	1.5	1.5	3.7	14.5	14.6	14.7
CMC3	2008	2.6	0.8	0.3	0.7	6.6	1.5	1.5	5.1	4.6	4.7
CMC4	2008	4.1	0.6	3.0	0.5	1.5	10.7	1.5	35.5	36.3	37.6
CMC5	2008	4.2	0.3	0.5	0.3	1.5	6.9	1.5	29.3	32.7	33.5
CMC6	2008	3.5	0.25	0.25	0.85	1.5	13.6	4.2	23.2	22.4	23.6

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); molar nitrogen to phosphorus ratios; benthic organic matter ash free dry mass; benthic and pond spill-over water chlorophyll *a* concentration. Values in parentheses were outliers not used in regression analyses and values with a period indicate no data. Site acronyms as in Table 1.

Site	NDS Limiting Nutrient		molar N:P Ratio		BOM AFDM (g/m ²)		Benthic chl <i>a</i> (mg/m ²)		Pond chl (µg/L)
	Up	Down	Up	Down	Up	Down	Up	Down	
WBC1	CO	N	406.88	271.78	10.90	8.49	4.32	4.86	0.079
WBC2	.	P	202.83	218.97	1.47	2.06	3.41	2.71	0.072
WBC4	CO	P	200.37	174.27	3.56	4.30	3.93	2.31	0.077
WBC5	CO	P	213.48	153.87	2.99	12.15	2.82	2.75	0.095
CMC1	N	CO	65.56	29.54	8.86	11.30	2.53	2.34	0.106
CMC2	N	CO	67.25	43.22	7.34	24.99	2.74	3.26	0.094
CMC3	CO	CO	17.29	31.17	6.83	8.74	3.25	1.92	0.212
CMC4	CO	N	157.20	151.14	(76.81)	(4.53)	9.29	5.70	0.173
CMC5	CO	CO	161.82	267.54	(5.26)	(76.81)	(3.25)	(9.72)	0.193
CMC6	CO	CO	71.18	208.94	13.13	8.45	2.94	2.84	0.218

Figure Headings

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

Fig. 2 Relationships between beaver pond morphology ratios ($\ln(\text{dam height (m)}/\text{pond surface area(ha)})$) and soluble reactive phosphorous (SRP) ratios (downstream concentration / upstream concentration) in 2007 and 2008 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. 2007 SRP ratios were significantly predicted by pond morphology (*solid black line*).

Fig. 3 Relationships between beaver pond morphology ratios ($\ln(\text{dam height (m)}/\text{pond surface area(ha)})$) and downstream/upstream ratios of (A) benthic chlorophyll *a*, (B) benthic organic matter (BOM) ash-free dry mass (AFDM), (C) pond 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 feeder invertebrates. Data points above the dashed lines indicate an increase in that variable downstream of beaver ponds and data points below indicate a decrease downstream of

beaver ponds. Significant prediction of dependent variable by pond morphology is indicated by the presence of a regression line.

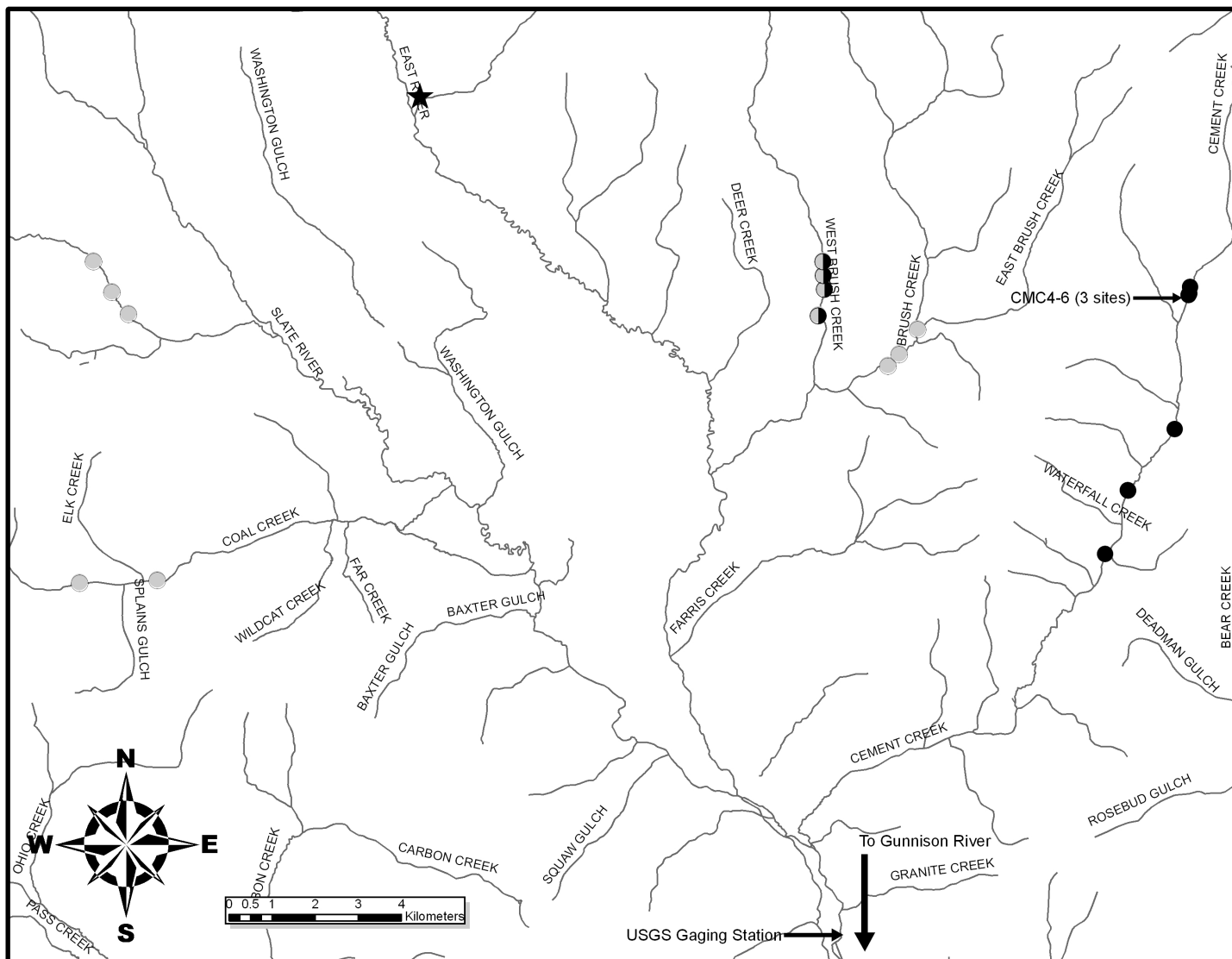


Fig. 1

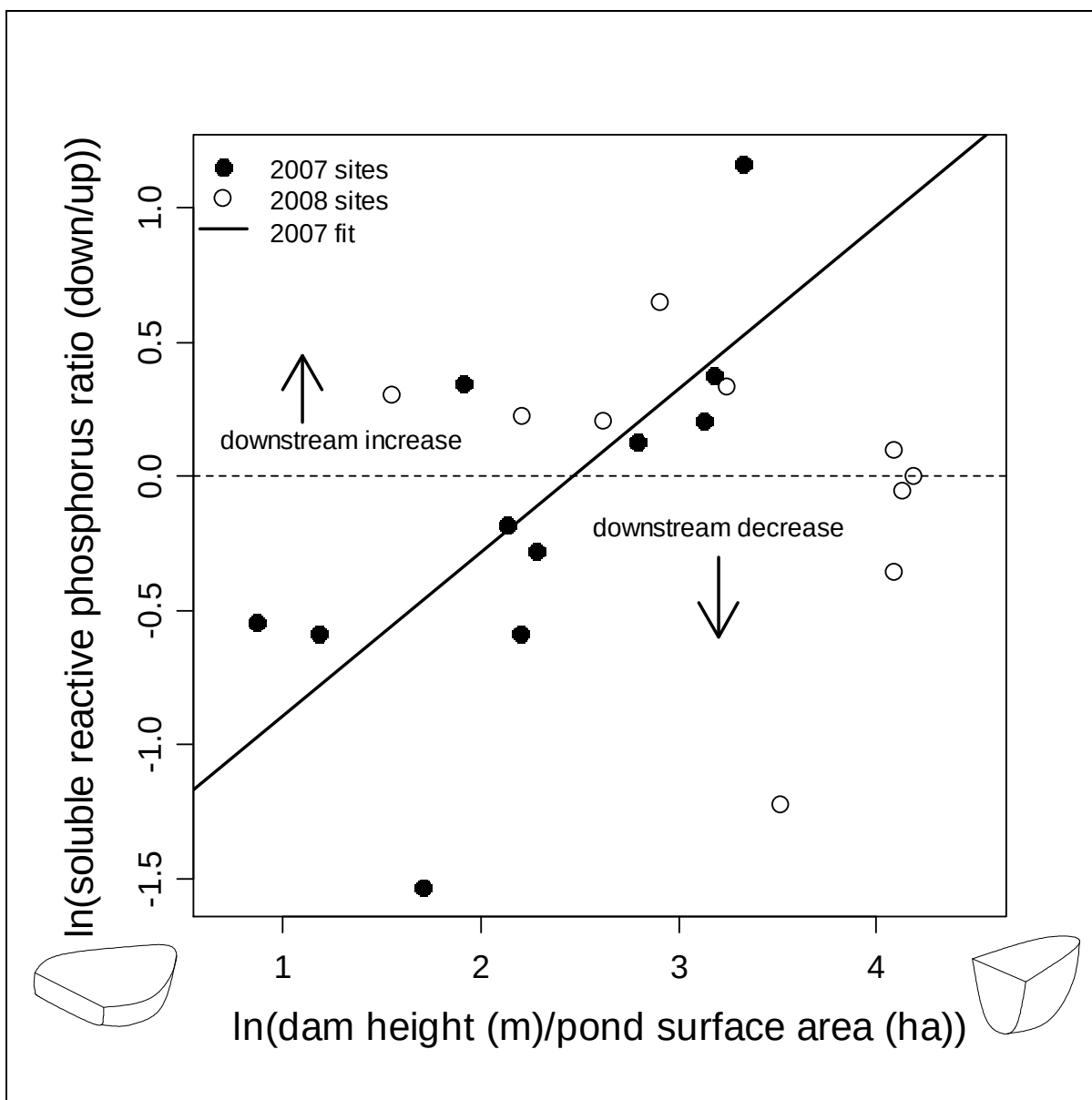


Fig. 2

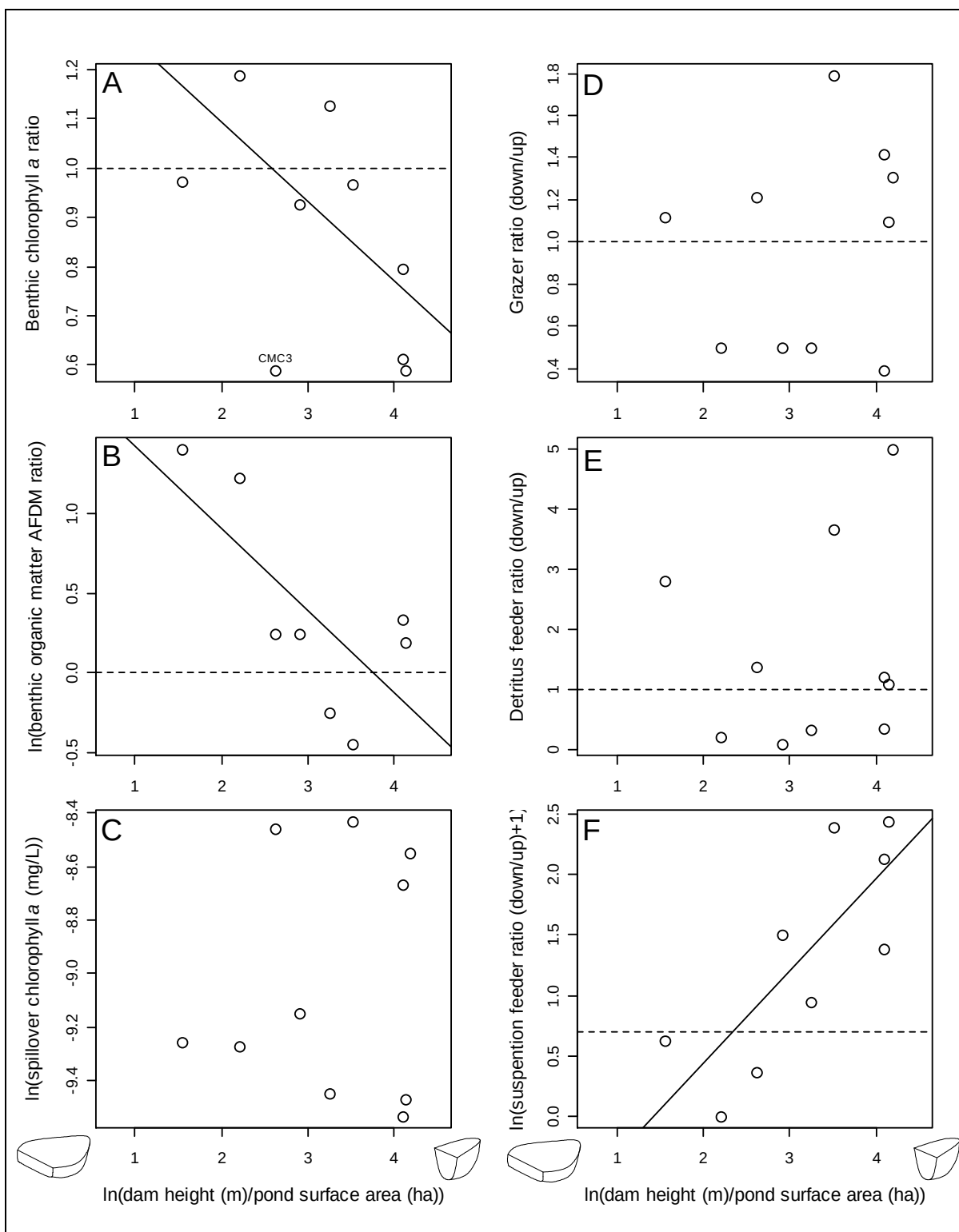


Fig. 3