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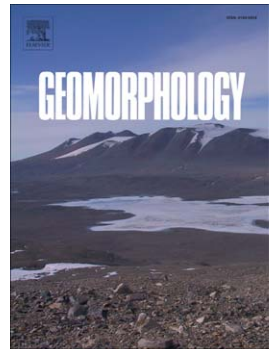

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Title

Classification of the alterations of beaver dams to headwater streams in northeastern Connecticut, U.S.A.

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Abstract

Of the many types of barriers to water flow, beaver dams are among the smallest, typically lasting less than a decade and rarely exceeding 1.5m in height. They are also among the most frequent and common obstructions in rivers, with a density often exceeding ten dams per km, a frequency of construction within a given network on a time scale of years, and a historic extent covering most of North America. Past quantification of the geomorphologic impact of beaver dams has primarily been limited to local impacts within individual impoundments and is of limited geographic scope. To assess the impact of beaver dams at larger scales, this study examines channel shape and sediment distribution in thirty river reaches in northeastern Connecticut, U.S.A. The study reaches fall within the broader categories of impounded and free-flowing segments, leaving a third segment class of beaver meadows requiring additional study. Each of the study reaches were classified at the reach scale as free-flowing, valley-wide beaver pond, in-channel beaver pond, and downstream of beaver dam. The bankfull channel width to depth ratios and channel widths normalized by watershed area vary significantly across the study reach classes. Additionally, reaches modified by beaver dams have finer sediment distributions. This paper provides the first quantitative geomorphic descriptions of the in-channel beaver pond and reaches downstream of beaver dams.

Given the different channel shapes and sediment distributions, we infer that geomorphic processes are longitudinally decoupled by these frequent barriers that control local base level. These barriers generate heterogeneity within a river network by greatly increasing the range of channel morphology and by generating patches controlled by different processes. Therefore, in spite of the small size of individual beaver dams, the cumulative effect of multiple dams has the potential to modify processes at larger spatial scales. To improve assessment of the larger-scale impacts, we propose a hierarchical classification scheme based on discontinuities, place the reach classes of this study within that scheme, and suggest that further research should continue investigation of discontinuity at the network scale and quantification of the cumulative impacts.

Keywords

fluvial geomorphology, *Castor canadensis*, fluvial discontinuity, base level, river restoration

1. Introduction

1.1. Rationale

Many processes interrupt the progression of a channel toward the equilibrium inherent in a graded river (*sensu* Gilbert, 1877; Davis, 1902), including those that add barriers to water flow and result in local increases in base level (e.g., Mackin, 1948, Leopold and Bull, 1979). The resulting river network is patchy across temporal and spatial scales (Poole, 2002). Of the many types of barriers in river networks, beaver dams are among the smallest in the temporal and spatial scales. The longevity of beaver dams generally ranges from years to decades (Naiman et al., 1988; Wright et al., 2002), and dam heights rarely exceed 1.5m (Gurnell, 1998). Beaver dams are also, however, among the most frequent obstructions to river flow. Beavers build new dams on the time scale of years (Fryxell, 2001), continuously disrupting the equilibrium of the short-term "steady time" envisioned by Schumm and Lichty (1965). Beaver dams are also ubiquitous and found at densities that often exceed ten dams per kilometer (Pollock et al., 2003), and historically numbering in the tens to hundreds of millions in pre-European North America (Butler and Malanson, 2005). North of the Mexican border, they were found in all North American biomes with the exception of peninsular Florida, the arid West, and the arctic (Pollock et al., 2003). Therefore, in spite of the small size of these features in relation to the continental scales of geomorphology, the cumulative local modifications to hydrologic and sediment budgets (Butler, 1995; Collen and Gibson, 2000; Pollock et al., 2003; Rosell et al., 2005) have the potential of modifying geomorphic processes at larger spatial scales (Gurnell, 1998).

Given the potential large-scale impacts, a need exists to document the geomorphology of streams affected by beaver dams, particularly when considering the applied practice of river restoration. Although the nature of beaver ponds is well recognized, there is limited quantification of the geomorphic impact of dam construction and that quantification is primarily focused on the ponds themselves (Butler, 1995; Butler and Malanson, 1995; Gurnell, 1998; Meentemeyer and Butler, 1999; Bigler et al., 2001). Only three studies address the larger scale, all of which are located in the U.S. Rockies (Persico and Meyer, 2009, Kramer et al., 2012, Polvi and Wohl, 2012). Overall, the literature documenting geomorphological impacts of beaver dams in North America is limited to the Pacific Northwest, Rocky Mountains, upper Midwest, and boreal Canada. Therefore, a need exists to both improve larger-scale understanding of beaver dam impacts as well as to increase the geographic range of these studies.

A need also exists to classify channels affected by discontinuities such as beaver dams because classification improves fundamental understanding of impacts of channel form on network processes (Schumm, 1985). Burchsted et al. (2010) propose a free-flowing – impoundment – meadow classification scheme where the impoundments and meadows may be generated by beaver dams or other discontinuities. We propose that evaluating these different categories in a network can help assess water, sediment and nutrient budgets as well as the corresponding habitat and fauna that are the focus of many restoration efforts (e.g., FISRWG 1998). In contrast, most commonly used classification schemes (e.g., Schumm, 1977; Rosgen, 1994; Montgomery and Buffington, 1997; Nanson and Knighton, 1996) generally focus on the subdivision of free-flowing channels that are typically in equilibrium. Overall, channels that fall within the impounded or meadow classes remain unrecognized at the fundamental level in these schemes. Minor exceptions include the following: Montgomery and Buffington (1997, p602), who include "forced morphologies" as a qualifier to apply to their free-flowing reach categories, such as "forced pool-riffle;" and channels through meadows that have aggraded to a new equilibrium and can be classified within the existing schemes. Stream evolution models describe the process by which channels return to a graded form following a change in base level (e.g., Schumm, 1993), however the intermediate types of channels within this transition are generally not included in classification schemes. Further, these models rightly focus on ultimate base level but they typically overlook changes to local base level. The implications of mistakenly assuming a free-flowing, equilibrium condition is demonstrated, in part, by Walter and Merritts (2008), who show that a well-known description of a meandering channel form is a channel adjusting to a change in local base level.

To address these needs, the objective of this study is to quantify the impacts of beaver dams on channel form and sediment distribution in comparison with free-flowing reaches. This objective is set within the larger goal of classification of river reaches that can be applied at the network scale. To do this, we test the null hypothesis that, in our study streams in the northeastern United States, channel form and sediment distribution in reaches that are dammed by beaver are the same as those in reaches unmodified by beaver. We then place the newly classified channel reaches within a hierarchical classification scheme of river networks (Burchsted et al., 2010).

1.2. Factors influencing the impact of beaver dams

Beavers build dams out of a range of materials including wood, green vegetation, impounded sediment, riparian soils, and stones ranging in size up to large cobbles (Müller-Schwarze and Sun, 2003). The dams are typically either set within existing channel banks or they extend beyond the original channel to the valley wall (Pullen, 1971). By acting as "a barrier across the path of the graded stream" that is rapidly created (Mackin, 1948, p496), these dams act as controls that increase local base level (Leopold and Bull, 1979). For the purposes of this paper, the term base level refers to "the theoretical limit or lowest level toward which erosion of the Earth's surface constantly progresses … the level below which a stream cannot erode its bed" (Neudendorf et al., 2005). Therefore, the base level set by a beaver dam is the height of the impounded water. Rapid increases in base level, such as those caused by dam construction, cause aggradation upstream and degradation downstream of the base level control (e.g., Mackin, 1948; Leopold and Bull, 1979).

Most beaver dams persist less than a decade (Gurnell, 1998). If a dam fails structurally, the resulting decrease in local base level generates downcutting that moves headward through the impounded sediments. The dam may also remain in place as the channel continues aggrading until it reaches a new equilibrium. In either case, the riparian zone affected by the aggradation transitions to a wet meadow with herbaceous vegetation growing on the previously impounded sediments (Naiman et al., 1988). As described in numerous reviews (Gurnell, 1998; Collen and Gibson, 2000; Pollock et al., 2003; Rosell et al., 2005; Burchsted et al., 2010), the impacts of the construction and failure of beaver dams include the following: modification of the local hydrologic regime through storage and release of water, increased evaporation from ponds, and altered flow paths; modification of the local sediment budget by deposition and subsequent erosion during catastrophic failure; modification of biogeochemical budgets and cycles through addition of nutrients and generation of anoxic conditions that alternate with oxygenated reaches; and creation of distinct habitat patches with very different species assemblages in beaver-modified areas.

The extent of beaver modification depends on the longevity of the colony. In this paper, we use Bradt's (1938) definition of a beaver colony as "a group of beavers occupying a pond or stretch of stream in common, utilizing a common food supply, and maintaining a common dam or dams." Following this definition, the beavers in a colony may live in one or more lodges built of wood and mud in the impoundment and may also live in one or more burrows dug into the banks. Although they live in close family units, all the beavers in a colony are not necessarily immediate family (Crawford et al., 2008; Fischer et al., 2010). Where beaver colonies persist, the beavers further modify the landscape beyond construction of a dam and creation of an impoundment. These modifications can include the following: continued dam construction, with three dams or more in a hundred-meter stream reach (e.g., Fig. 1B); felling trees and importing wood from riparian or nearby upland zones for lodge and dam construction and for storage as a winter food source (Müller-Schwarze and Sun, 2003); generation of a sediment source into the impoundment through the digging of canals, burrows, and the creation of slides (Meentemeyer et al., 1998); and excavation of impounded sediment near lodges and submerged food caches.

Although most beaver dams last less than a decade, a significant percentage of beaver colonies can persist. For example, 20% of the Appalachian colonies studied by Fryxell (2001) persisted beyond the 11-year study period. The longevity of a beaver colony decreases with increasing channel gradient. Long-term persistence requires a channel size sufficient to generate a pond when dammed as well as water supply throughout the year (Howard and Larson, 1985; Beier and Barrett, 1987; Gurnell, 1998; Pollock et al., 2003) or a natural water body such as a lake (Wright et al., 2004). Variables controlling water supply include climate (Persico and Meyer, 2009), drainage area, and soil type (Howard and Larson, 1985). Beavers build dams regardless of food availability, with no significant relationship found between food and dam construction, however, the amount and type of food determine the size and longevity of the colony (Howard and Larson, 1985; Beier and Barrett, 1987; Fryxell, 2001; Smith and Tyers, 2008; Harrison 2011).

1.3. Regional setting

This study is located within the northeastern uplands of Connecticut (Fig. 1). The study area has a relief of 225m and is primarily forested with a mix of coniferous and deciduous trees. The streambeds of free-flowing channels are primarily subangular to subrounded gravel to cobble with occasional exposures of granitic gneiss or schist bedrock. The corresponding bedforms generally fall within the plane bed classification (Montgomery and Buffington, 1997), with steeper reaches falling in the step-pool and, occasionally, the cascade class. These streams are incised in valleys with thin mantles of coarse ablation till.

The climate is temperate, with strong seasonal variability in temperature. Mean annual rainfall is 1300mm, with approximately equal distribution throughout the year, and a mean annual runoff of 600mm/yr (Weiss and Cervione, 1986). Floods occur year-round. They are generated by rainfall in combination with snowmelt in the winter and spring, local thunderstorms in summer, and tropical storms in late summer and fall. Low flows occur during the late summer and early fall

(Weiss and Cervione, 1986). Catchments with coarse meltwater deposits covering more than 20% of the area sustain higher baseflows than those with fewer meltwater deposits (Armstrong et al., 2004).

The northeastern United States was densely populated by beaver prior to European settlement. Beaver furs were so valuable to Europeans—and so plentiful in the European colonies—that their harvest and sale were primarily responsible for financing the colonies (Dolin, 2010). Nearly ten thousand beaver skins were shipped from 1652-1658 out of a Springfield trading post, less than 65 km from the study area, with additional nearby trading sites in Windsor and Hartford (Müller-Schwarze and Sun, 2003). The insatiable appetite for beaver fur led to the extirpation of beaver from the east coast by 1675 (Thorson, 2009).

Native Americans also trapped beaver prior to European settlement (Dolin, 2010). The extensive beaver populations of the 17th century may have been anomalously high, following the loss of more than 90% of the Native American population to disease spread by the earliest European contact (Mann, 2005). Historical research by Mann (2005) strongly suggests that wildlife populations increased rapidly as the land was depopulated of the native people.

Regardless of the pre-European history, beaver were undoubtedly extirpated from the region in the 17th century. They were reintroduced by wildlife managers in the early 20th century. The first pair of beaver were released in 1914 in Union, Connecticut (CTDEP, 2000), in the north of the study area. Beaver populations have since dramatically expanded in the state, with no suitable stream uncolonized. The State of Connecticut currently permits the harvest of beaver in state forests by licensed trappers and manages colonies outside of the state forests on a case-by-case basis (CTDEP, 2000).

Human management has also modified the study landscape at large. The landscape history since European colonization includes near-total deforestation for crops, pasture, and fuel, with forest regeneration beginning approximately 150 years ago (Cronon, 1983). The rivers in the study area were presumably straightened as part of the agricultural development that accompanied settlement (e.g. Mattingly et al. 1993). We expect that pre-European longitudinal discontinuities have been primarily removed and that some have been hardened by construction of dams and roads, in-stream large wood loads have been reduced or eliminated (Costigan and Daniels, in press), and the productive bottomlands have been converted to agriculture, similar to the recorded histories of western rivers (e.g., Lichatowich, 1999; Wohl, 2005).

2. Methods

To test the hypothesis that beaver dams alter the shape and sediment distribution of channels, we compared channel shape parameters and sediment distribution in free-flowing reaches and in reaches modified by beaver dams in the summers of 2008 – 2010. Each reach was classified as free-flowing, valley-wide beaver pond, in-channel beaver pond, or downstream of beaver dam (Fig. 2). The following section describes the study reaches and classification and the subsequent section describes the data collection.

2.1. Study site and channel reach classification

The thirty study reaches are located on four low order (<4) headwater streams in the study area (Fig. 1 and Table 1). All reaches are located in nearly entirely forested catchments with minimal modern human impact. Although woodlots are currently actively harvested in the area, no significant visible logging has occurred within the catchments of the study sites. Many study reaches are set within state forest property boundaries, where beaver harvest is permitted without limit in winter months by state-licensed trappers. Reaches 4.011–4.22 are located within the Yale-Myers Forest, where beaver trapping is not permitted under any circumstances.

The study reaches drain catchments from 0.25-52.15 km^2 in size (Table 1) with valley gradients ranging from 0.1 to 4.8%. The catchments draining to all of the study reaches have limited meltwater deposits and fall within the low baseflow class. Each reach is approximately 100m in length, with the upstream and downstream limits set by geomorphic features such as bedrock constrictions, changes in gradient, or beaver dams. We assigned each reach to one of four classes based on the nature of modification by beaver dams, as described below.

Free-flowing. The free-flowing (FF) river class applies to the unobstructed alluvial headwater channel that is most commonly used as a reference for river restoration (FISRWG, 1998; Burchsted et al., 2010). This type of stream can be further classified into additional categories (e.g., Montgomery and Buffington 1997), which is not necessary for the sake of this study. The reaches in this study category have high to saturated oxygen levels, a high percentage of coverage by the forested canopy, a large mineral substrate that decreases in size with distance downstream, and a small width that increases with distance downstream. These properties are in accordance with the headwater stream described within the River Continuum Concept (RCC) (Vannote et al., 1980), which is built on the geomorphic principles of channel size dependency on discharge and corresponding distance from headwaters (Leopold and Maddock 1953). Although subsequent theoretical work has added complexity to the headwater network (e.g., Montgomery, 1999; Benda et al., 2004), this reach class falls entirely within the characteristics of the headwater channel described by earlier work.

Valley-wide beaver ponds. Beaver dams that extend beyond the stream banks to the valley wall create valley-wide beaver ponds (VWP). These ponds frequently have standing dead wood from the forest flooded by the beaver dam. These reaches are low-velocity, depositional reaches, often with hypoxic water and sediments (Naiman et al., 1988; Snodgrass and Meffe, 1998), and can be subclassified according to age and dam condition (Pullen, 1971; Woo and Waddington, 1990; Snodgrass and Meffe, 1998). Beaver dams are often leaky, with the amount of water leaking through the dam increasing with age. In addition, vegetation often grows on the leaky older dams, forcing the stream to flow entirely through lushly vegetated organic matter for several meters. Various types of incomplete breaches may occur before the dam fails (Woo and Waddington, 1990), decreasing water levels in the impoundment.

In-channel beaver ponds. In-channel beaver ponds (ICP) are created by beaver dams limited to the bankfull channel. ICPs frequently occur in series, with each pond extending to the face of the next dam upstream and a valley-wide beaver dam forming the upstream limit of the series. In-channel dams appear to be constructed with less effort than valley-wide dams, with fewer materials overall and with less mud on the upstream face resulting in a leakier structure and a higher failure rate. ICPs range from several meters to tens of meters in length and are often set within wet meadows. The meadow vegetation may be growing on previously impounded sediments or may be supported by the associated raised groundwater table. In either case, the riparian zone is typically lushly vegetated.

Downstream of beaver dams. Valley-wide beaver dams appear to modify the reaches downstream of these dams (DD). In some cases, these reaches are impounded by smaller in-channel beaver dams, and would be classified as in-channel beaver ponds (ICP: see above). Where the reach is not impounded, the channel downstream of the dam has a multi-channeled morphology with numerous channel threads that converge some distance downstream (Woo and Waddington, 1990; John and Klein, 2004; Westbrook et al., 2006; Polvi and Wohl, 2012).

For any given network, the above reach classes are approximately 100m in length and can be hierarchically set within segment classes that are hundreds to 1000m in length. In a network colonized by beaver, the three main segment classes described by Burchsted et al. (2010) are free-flowing, impoundment, and meadow. In this study, the FF and DD reach classes fall within the free-flowing segment class, and VWP and ICP fall within the impounded segment class. Because a sufficient sample size is necessary for statistical analysis of these reach classes, reaches falling within the beaver meadow segment class were not included in the study and require further study.

2.2. Data collection and analysis

Within each study reach, several cross-sections were surveyed using standard rod, level and tape techniques. The surveyed points at each cross-section were selected to define the bankfull and active channels. Where the channel was set within a floodplain, bankfull stage was identified in the field following Wolman (1955), where the break in slope between the channel bank and adjacent floodplain was visually identified in the field as the point of minimum width : depth. Bankfull stage for impounded and entrenched channels could not be defined in this way. In those cases, bankfull stage was defined in the field according to evidence of regular inundation, such as absence of living tree roots and regular fluvial mobilization (erosion or deposition) of sediments.

In contrast to the bankfull channel—intended to describe a basic channel shape that might represent underlying geomorphic processes—the active channel was defined as the channel that provides habitat to instream organisms. Identification of this channel is critical for river restoration design focused on species restoration such as cold-water fish (e.g., FISRWG, 1998). Selection of the active channel edge followed Wilkins and Snyder (2011), where the boundary is located at the break between emergent aquatic vegetation and riparian vegetation. In every case, the thalweg was also surveyed to determine the depth of the active and bankfull channels.

The substrate clast size was visually categorized at each surveyed point and at three points equally spaced across the active channel bed. Percent embeddedness of coarse substrate was visually estimated in cases where sand or finer substrate less than 3cm in depth overlaid a coarser material. If the overlying fine substrate was present along the cross-section for at least one meter and was at least 3cm in depth (a situation particularly common in, but not limited to, impounded reaches), that material was considered the substrate. If the streambed at a point was considered embedded, the underlying clast size was recorded as the main substrate. The size of the embedding material was recorded as a secondary type of substrate. Cumulative sediment distributions were determined for each reach based on all substrate observations in that reach. Sediment distributions were further determined for each reach class based on combined observations for all reaches in that class. In cases of embedded substrate, the fine and coarse clast sizes were both included in the sediment distributions.

Ground measurements of channel morphology were complicated by certain circumstances. In valley-wide ponds, channel bed elevations were recorded as depth from the water surface, and active channel widths were determined from aerial images. In these cases, field measurements were taken to determine the distances between the active channel edge, which would be visible in aerial images, and the edge of the bankfull channel, which would not (e.g., Wilkins and Snyder 2011). In reaches with mid-channel alluvial bars set within the bankfull channel, the active channel on each side of the bar was surveyed separately. The active channel parameters at those cross-sections were determined by considering the whole stream to be a composite of the two channels on each side of the bar (i.e., active stream width equals the combined active width of the two channels). In locations where the channel was multi-threaded, with incised bankfull channels separated by vegetated glacial till, stream parameters were determined from the main channel thread alone. Where the channel banks were vertical, the elevation at the top and bottom of the bank was measured and the higher elevation was used to calculate channel depth. Where the substrate was unconsolidated and soft, common in the highly organic sediments in impoundments, two elevations were also recorded. The higher elevation, corresponding to the estimated top of sediment, was used for calculation of morphology parameters.

Active and bankfull widths were calculated for each cross-section (Table 2). Active and bankfull depths were calculated by subtracting the thalweg elevation from the active and bankfull elevations. The depths for both banks at each cross-section were averaged to determine the corresponding depth at that cross-section. These values were used to determine width to depth ratios (w:d) and width normalized by the square root of the catchment area (w/sqrt(A)). The square root of the catchment area was used to normalize channel widths to accommodate the two orders of magnitude spanned by the range of catchment areas for the study reaches. These values were calculated for each cross-section, and the mean value was calculated for each reach.

In addition to the survey data, the number of side channels was recorded at each cross-section. A total count was generated for each reach where side channels that connected cross-sections were only counted once. The riparian vegetation for each side of the channel was classified as forest, shrub or herbaceous. GPS readings and digital photographs were also taken at each study reach. The GPS points were imported into ArcGIS 10.0. The catchment for each reach was delineated in the GIS by modifying existing subregional basin boundaries (CT DEP 1988) as needed, based on the 10ft (3.048m) contours of the 1:24000 USGS topographic maps. The resulting catchment area was calculated for each reach. Valley gradient for each reach was calculated in the GIS from LiDAR point clouds with 60.1m (20ft) postings (Meyer, 2008). When a study reach contained a beaver dam, the elevation below the dam and above the impoundment was used to calculate reach slope.

The data were used to test the null hypothesis that channel form and sediment are indistinguishable between all types of reaches. We used the calculated channel width, depth, and w:d values as parameters of channel shape. We controlled for common parameters responsible for channel morphology in the following ways: controlling land cover and sediment supply by choosing study reaches within forested catchments with well-developed forest soils over a thin layer of coarse ablation till and shallow granitic metamorphic bedrock; controlling for catchment size by using dimensionless parameters in morphology analysis; and including valley slope in our analysis as a controlling variable. We compared whole populations of one reach class with another by comparing mean values for each reach, where the derived parameter for each cross-section was averaged across the reach. We used mean reach values to minimize the dependence of the samples on each other while improving the representation of each reach with multiple cross-sections. We used ANOVA tests of differences between means of multiple groups. Where those tests showed significant difference, we used t-tests of differences between means of two groups, and F-tests of equality of variances to determine statistical difference in channel shape between FF and other channel class populations at significance levels of 0.05 and 0.10.

3. Results

Tables 1 and 2 show the reach characterization data and channel shape parameters for each reach. Although slope varies significantly across reach classes (Fig. 3), it has a low correlation with channel morphology (Fig. 4). This correlation is significant for bankfull w:d ($t(20)=-1.97$, $p=0.06$) and active w/sqrt(A) ($t(21)=-1.91$, $p=0.07$), however, it is not significant for any morphology parameter when the VWP class is excluded from analysis. Reach classes, on the other hand, do have significant differences in mean bankfull w:d ($F(3,24)=5.46$, $p=0.005$) and w/sqrt(A) ($F(3,24)=8.62$, $p<0.001$) (Fig. 5), rejecting the null hypothesis that reach channel form is the same regardless of beaver modification. Comparisons for the active channel were less conclusive than for the bankfull channel. A significant difference exists between types of channels for w/sqrt(A) ($F(3,24)=4.72$,$p=0.01$) for the active channel, but not for w:d ($F(3,24)=0.98$, $p=0.42$).

The channel shape of the FF reach class was also compared separately with each of the other three reach classes. Bankfull w:d for VWP and ICP, but not for DD, is significantly different from the free-flowing channel (FF vs.: DD $t(12)=-0.18$, $p=0.4$; VWP $t(11)=-2.79$, $p=0.009$; ICP $t(8)=1.83$, $p=0.05$), and w/sqrt(A) is significantly different only for VWP (FF vs.: DD $t(12)=-0.86$, $p=0.20$; VWP $t(8)=-3.66$, $p=0.003$; ICP $t(11)=0.00$, $p=0.50$). The active channel, on the other hand, is essentially indistinguishable between FF and other classes. Only VWP w/sqrt(A) has a significantly different mean ($t(8)=-2.63$, $p=0.02$). Tests of variation in channel shape show significant differences. We expected to find greater variation in the reaches modified by beavers. Every parameter examined for VWP has greater variation than FF (Fig. 5). The DD class has greater variability for active w:d and bankfull w/sqrt(A). Surprisingly, the only finding for ICP is decreased variance in bankfull w:d.

To examine the local effects of the dams, which we hypothesized would dissipate with distance from the barrier, we compared channel shape across reaches at certain locations (Table 3). Variance in bankfull w:d for a given cross-section location is significantly different from the FF type in every case except the ICP downstream cross-section. As expected, VWP is both more variable than FF and has larger w:d ratios at all locations along the reach. The same is true for DD reaches for the upstream and downstream channel locations. Surprisingly, however, the DD central transects have very low variability. Given the high levels of variability in the other locations for these reaches, the net result for the reach class as a whole is equivocal. The significantly greater variability at the upstream cross-section, which is immediately downstream of the beaver dam and is typically a multi-thread channel, is likely a true positive given the complexity of the channel at these locations. Unlike the equivocal finding in DD variation, ICP has lower variability of bankfull w:d in two of the three cross-section locations. This is consistent with the lower overall variability in ICP versus FF reaches. Similar to the results of reach comparisons using averaged cross-section data, active channel w:d results show no significant difference across channel types. Although some scattered significant results exist when individual types of channels are compared with FF (Table 3), these results do not provide a coherent pattern.

The distribution of channel bed sediments for the four types of reaches also show distinct differences (Fig. 6). Unsurprisingly, VWP has much finer sediment than FF, with essentially no overlap between the VWP reach with the coarsest sediment and the FF reach with the finest sediment. The DD class, on the other hand, is very similar in sediment size to FF, with greater occurrence of fine sediments. This contradicts the hypothesis that DD sediments would be coarser because of the steeper valley gradient of these reaches (Fig. 3). Lastly, the ICP class is distinct from the other classes, overlapping the coarse end of the range of VWP and the fine end of the range of FF. This is consistent with the interpretation that the ICP class consists of a mix of depositional and erosional patches.

4. Discussion

4.1. Reach classification

Overall, the parameters that successfully distinguish the classes of the study reaches are valley gradient, bankfull shape (w:d and w/sqrt(A)), and grain size distribution. Active channel shape was surprisingly ineffective at distinguishing channel classes, which is discussed in more detail below. The resulting qualitative description of the three beaver-generated classes is provided in Table 4.

The most unsurprising results of this study are those of the VWP. It is well known that beaver impoundments are wider and have finer sediments than free-flowing reaches. VWP reaches are significantly wider and have sediments that are nearly entirely finer than the FF reaches. The clear difference in VWP channel width is not explained by valley slope, where FF reaches at similar low gradients have much lower values for bankfull w:d and w/sqrt(A) and gradient has a very low correlation with channel shape parameters overall (Fig 4). Additionally, although the low correlations between gradient and channel shape are significant in two cases, that significance disappears when the VWP reaches are excluded from analysis, further demonstrating the greater influence of the VWP class on channel morphology.

Although the shape of the valley-wide ponds is statistically different, these shape parameters also have tremendous variability. We attribute the lack of difference in active channel shape in part to the wide variability in the VWP active channel, suggesting that this group could be split. We suggest a split in the VWP reach class according to the condition of the dam. For example, in reach 4.06, which is the impoundment of an abandoned and very leaky valley-wide beaver dam, a stream channel is incising into the sediments previously impounded when the dam was newer, better maintained, and more watertight (Fig. 7). The erosion associated with this incision has also continued into the flooded soils that predated the original dam (Fig. 7A). The relatively narrow active channel of this example contrasts with the very wide channel created by a well-maintained beaver dam (e.g., Fig. 2D).

Differences between the ponds associated with abandoned and active dams are captured in a plot of active versus bankfull w:d (Fig. 8). The valley-wide ponds with intact dams have very little difference between the bankfull and active channels because the dams are relatively water-tight and maintain a fairly constant base level throughout the year. Therefore, these reaches have nearly identical w:d ratios, both of which are very high. When the dams are abandoned, however, the increasing leakiness results in a slowly declining local base level at the dam. The channels respond by incising into the impounded sediments. In these cases, the bankfull channels have high w:d ratios because the dams still impound water under higher flows (e.g., more frequent than the 1.5 to 2-year storm). During lower flows, however, w:d ratios decrease dramatically as water leaks through the dams, base levels drop, and the streams returns to their beds within the newly excavated banks. This results in the unusual situation where the active w:d is much smaller than bankfull w:d for these reaches. Unfortunately, the VWP sample size in this study is insufficient to test the utility of this proposed subclassification, which warrants further investigation.

Although the basic form of the valley-wide beaver pond has been previously studied and quantified, the river forms and sediment characteristics associated with the DD and ICP reach classes are less well studied, with only qualitative observations (Pullen, 1971; Woo and Waddington, 1990; John and Klein, 2004). ICP reaches are typically a series of small ponds created by dams set within the bankfull channel downstream of a valley-wide dam. They have smaller w:d ratios and finer sediment than the free-flowing class but coarser sediment than in VWP. The stream banks typically have dense herbaceous or shrub vegetation unlike the forested banks of the free-flowing class.

In contrast with ICP, the DD reach is located downstream of a valley-wide beaver dam where no secondary downstream dams occur. This type of reach is found at steeper valley slopes than the ICP class (Fig. 3). This is consistent with the studies showing that beaver prefer and are more successful in valleys with shallower slopes (Gurnell, 1998; Pollock et al., 2003) and with our data that show that the VWP class is found at the lowest slopes (Fig. 3). We infer that valley-wide dams that are built just upstream of steeper valleys support colonies with shorter life spans that have less opportunity to construct secondary in-channel dams. This reach class has a multi-thread channel planform (Fig. 3A), with the side channels apparently created from avulsion generated by construction of the upstream dam (Nanson and Knighton, 1996). Despite the difference in planform, however, the shape of the main channel thread in the DD class is indistinguishable from the free-flowing reach and both types of channels have forested banks. DD reaches have patches of finer sediments not found in free-flowing reaches, which is more notable when considering that the valley slopes of the DD class are comparable with the steepest free-flowing reaches. This suggests that the DD reaches may store small pockets of fine sediments mobilized from upstream ponds between high flow events or eroded from the banks within the reach.

Although beaver-modified reaches generally have greater variability than free-flowing ones, the variability of the in-channel pond class is lower than that of the free-flowing class. We interpret these results as a reflection of the short spatial and temporal cycle of sediment mobilization and deposition caused by the frequent construction and breaching of the dams on a time scale of years. Following a breach, the channel incises into the previously impounded sediments. Because the ICP banks are far more cohesive than the bed due to dense bank vegetation, the channel undergoes downcutting instead of widening. Similar banks without vegetation widen instead (Smith, 1976; Smith, 2007). In a free-flowing reach, however, the channel bed is armored with coarse substrate and sediment mobilization occurs primarily on the banks. Sediment eroded from the banks is coarse enough to be easily re-deposited downstream, potentially within the same reach in lower velocity zones, generating lateral variability. In contrast, the relatively fine, previously impounded sediments of the in-channel ponds are transported completely out of the reach once mobilized. The sediment observations support the interpretation of aggradation and degradation, with fine and coarse sediment found in ICP reaches (Fig. 6).

In keeping with the interpretation of cyclic deposition of sediments and subsequent incision into those sediments, bankfull w:d for ICP is significantly smaller than for the free-flowing class. An alternative interpretation of the lower w:d values is that beaver preferentially select channels with lower w:d ratios for construction of in-channel dams. This explanation, however, seems unlikely because the locations of ICP reaches are strongly controlled by the presence of valley-wide dams and valley gradient. The ICP reaches are in significantly shallower valleys than FF. In the absence of beaver, these valleys would tend to have greater widths and higher w:d ratios. Additionally, Howard and Larson (1985) show that the density of beaver dams in headwater streams is positively correlated with stream width while negatively correlated with—and limited by—channel gradient. Because beaver dams are constructed in high densities at high stream widths, it cannot be that the beavers are selecting reaches with low w:d to build their high density in-channel dams. Therefore, we interpret the low bankfull w:d values of ICP reaches as a result of beaver activity rather than as a reflection of site selection by the beaver.

4.2. Network-scale classification

Following our previous work (Burchsted et al., 2010), we suggest an organizational structure of free-flowing, impounded, and meadow channel segments set within the river network scale (Fig. 9), which roughly corresponds with the graded, aggrading, and degrading classes of Mackin (1948). Reaches in the free-flowing class are generally in a dynamic equilibrium or graded condition. The

FF and DD reach classes, defined in this paper, as well as most existing classification schemes (e.g., Schumm, 1977; Rosgen, 1994; Montgomery and Buffington, 1997; Nanson and Knighton, 1996) primarily fall within the free-flowing segment class. Unlike most of the reach classes within this segment class, the DD reach is considered to be down-cutting. Based on the comparisons between DD and FF reaches in this paper, erosion within the DD reaches appears to be primarily limited to creation of a multi-thread planform—through generation of new channels or excavation of paleochannels—rather than eroding an established channel.

The impounded segment class encompasses reaches that have had a rapid increase in base level and are actively aggrading. The VWP and ICP reaches of this paper fall within the impounded segment class. Further investigation is needed determine whether the VWP class that is presented in this paper should be split into two separate classes based on dam condition, where unmaintained dams promote erosion of a channel into impounded sediments.

The meadow segment class is largely unstudied. We propose that it would include at least two major reach classes. In one, the beaver dam remains in place and the impoundment has filled in with sediments to the point that the channel has returned to a dynamic equilibrium. At this point, the impounded sediments typically support herbaceous vegetation. The second reach class would be actively degrading following a breach in the beaver dam. Future research should examine reaches falling within this category in sufficient detail to categorize them as well as the other two segment classes.

Classification of segments across a river network is necessary to determine the level of complexity in the network. Although simplified free-flowing channels are generally considered visually attractive and dominate many modern river networks, these forms do not provide the functions of historic channels with greater complexity (Wohl, 2005). In contrast to river networks comprised primarily of free-flowing segments, networks that include impounded and meadow channel segments will have frequently decoupled segments with additional processes that provide critical ecological functions. Determining the heterogeneity of segment and reach classes longitudinally along the river channel can help quantify this complexity, once an adequate classification system has been created. Rivers can also be heterogeneous laterally across the valley, particularly in systems where log jams create multiple channel threads, each of which has its own longitudinal heterogeneity (e.g., Collins et al., 2002). The heterogeneity across these river valleys may be equally important to heterogeneity along the valley, because the side channels, channel edges, and increased floodplain connectivity associated with these anastomosing channel forms also support critical habitat (Collins et al. 2002).

4.3. Implications

The concept of patchy erosion and deposition associated with beaver dams can help resolve the conflicting results between studies of the sedimentary record (Persico and Meyer, 2009; Kramer et al., 2011; Polvi and Wohl, 2012) and modern ponds (Butler and Malanson, 1995; Meentemeyer and Butler, 1999; John and Klein, 2004; Pollock et al., 2007). On the one hand, examination of modern beaver ponds shows that sediments accumulate at very high rates and suggests that beaver dams are a potent geomorphic agent. Studies of the sedimentary record, however, show that total accumulation of sediment impounded by beaver dams since the last glaciation rarely exceeds 2m, and these sediments do not continually accumulate. They accumulate to greater thickness only where they fill in discrete post-glacial depressions in the channel profile. The short lifespan of beaver ponds may be sufficient to explain the lack of continued sediment accumulation. We suggest that the incision and bank erosion that is associated with prolonged failure of valley-wide ponds and cyclic failure of in-channel ponds may also play a role not yet understood or quantified.

Although beaver dams are unlikely to modify sediment budgets at long time scales, they may be sufficient to alter the timing and nature of delivery of sediments. The failure of one beaver dam is capable of generating a series of failures downstream, increasing the rate of peak flow and mobilization of sediment accordingly (Butler, 1989). These dams, therefore, play a significant role in the generation of channel form in the ways documented in this article as well as by increasing the frequency of high runoff rates beyond those predicted by meteorological patterns or past hydrologic data of channels without beavers.

Channel form is typically quantified with measurements of the bankfull channel. The traditional geomorphic meaning of bankfull channel, however, is changed in reaches modified by beavers. This is particularly true in the VWP class, where the channel "banks" are simply determined by the lateral extent of water impounded by the dam. In these reaches, no clear break in cross-sectional slope exists between the channel bed, its banks, and the valley floor. New banks can be created in these ponds by subsequent channel incision or as the channel reaches a stable equilibrium following aggradation. In the former case, local base level provides the dominant control over channel shape. Because the construction and failure of these base level controls occur at a time scale of years, the patterns of change of these small, frequent discontinuities affect channel shape as much as the flood-related sediment transport that is traditionally considered to determine bankfull channel shape.

The active channel is not commonly used in the geomorphic literature to describe channel form. Although the active channel is statistically the same across the reach classes in this study, the data support dividing the valley-wide pond class into separate maintained and abandoned pond classes. This division should be studied further. Active channel morphology should also continue to be studied because of its importance to instream habitat and as a design parameter in river restoration. Unlike the bankfull channel, remote measurements of active channel width correlate well with field data (Wilkins and Snyder, 2010), which is of great benefit in creating methods for assessment of rivers at the network scale.

5. Conclusions

Beaver dams create channel reaches with sediment size and channel shape well outside of the range of values measured for similar free-flowing channels. The long-term sediment storage generated by these frequent, small-scale features is sufficient to alter the channel shape, bed sediments, and corresponding habitat within a river network, which is of critical importance to river management. It is also likely that they alter the amounts and timing of the peak delivery of water and sediments.

To better classify networks with discontinuities, such as beaver dams, that control local base level, this paper presents geomorphic data that compares free-flowing stream reaches with those modified by beaver dams. The data support the creation of at least three separate classes of beaver-modified stream reaches: valley-wide beaver ponds, in-channel beaver ponds, and reaches downstream of beaver dams. The latter two are new reach classes to be quantitatively described in the geomorphic literature. The data also suggest a division of valley-wide beaver ponds into two separate classes based on dam condition, which requires further study. We further propose a hierarchical classification of river networks that places the reach classes of this study—as well as the reach classes in other schemes—within three fundamental segment classes of free-flowing, locally impounded, and meadow. Additional research is particularly required to classify the types of reaches within the meadow segment class.

At the network scale, stream complexity is greater in channels unaltered by modern human activity than in the more familiar modern forms which emphasize the free-flowing segment class (e.g., Wohl, 2005). River management can increase complexity at the network scale by adding additional segments types to the network. This would increase the complexity of the patchwork in the network, increasing habitat heterogeneity and providing essential habitat for many desired species that drive the billion-dollar river restoration industry (e.g., Pollock et al., 2004). Tools that quantify network-scale complexity, including classification of reaches within the network, are needed for fluvial geomorphology to continue contributions to ongoing river management and restoration efforts in the U.S. and across the world.

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Captions

Fig. 1. Locations of study reaches.

Fig. 2. Examples of the reach classes used in this study. A—free-flowing channel (FF). B—plan view of downstream of beaver dam (DD) showing multiple channel threads (arrows). Flow is to the south. Thick white lines show beaver dams. Light grey lines show edges of beaver-modified habitat. Dark grey lines show channels. Note tributary to the east joins the main channel in a beaver meadow at the southern border of this image. Northern-most side channel downstream of the main dam joins this tributary above the confluence. C—downstream of beaver dam (DD) main channel; D—valley-wide pond (VWP) with beaver dam (white arrow); E—in-channel beaver pond (ICP) located downstream from D.

Fig. 3. Properties of channel reaches. A—histograms of side channel count according to reach class; B— valley gradient across reach classes (ANOVA $F(3,24)=2.84$, $p=0.06$). Dashed grey line separates FF class from the other classes being compared with it. Labeled boxes have statistically significant differences from FF class as determined by pairwise t-tests ($p<0.1$)): m—significantly different means between reach classes; v—significantly different variance of means between reaches; *—modifier indicates greater significance ($p<0.05$).

Fig. 4. Low correlation between channel shape and valley gradient. Legend at bottom applies to all graphs. Trendlines and R^2 values apply to linear regressions of ln(w:d) and ln(w/sqrt(A)) vs. gradient for all reaches (“All reaches”) and for all reaches except VWP (“No VWP”). *—significant non-zero slope of regression line ($p<0.1$).

Fig. 5. Reach morphology based on means of cross-sections measured for each reach. Boxes show 2nd and 3rd quartiles, with whiskers showing maximum and minimum values. Dashed grey lines separate FF class from the other classes being compared with it. See Fig 3 caption for box labels.

Fig. 6. Cumulative sediment distributions based on visual classification of grain size at each surveyed cross-section point. Sediment size classes: COM—coarse organic material (e.g., wood, roots); OM—partially decomposed organic material; Si—silt (<0.06mm); Sa—sand (0.06-2mm); GF—fine gravel (2-16mm); GC—coarse gravel (16-64mm); Cb—cobble (64-256mm); Bl—boulder (>256mm). Chart A—distributions for all points combined for each class; B—range of DD (lines) and FF (shaded) distributions for individual reaches; C—range of VWP (lines) and FF (shaded) distributions; D—range of ICP (lines) compared with the VWP and FF (both shaded) distributions.

Fig. 7. Impoundment of a partially breached valley-wide beaver dam with an incising channel, where the partial breach results from an increase in leakiness in the dam as it ages following abandonment by the beavers. A—Stream bank near the beaver dam, with flow to the right. Arrow points out exposed tree roots of standing dead wood above the modern water surface. These roots had required soil for growth. Approximate pre-impoundment soil level, based on the height of the roots, is marked with the white line. Similarly exposed tree roots line both channel banks in the lower section of this impoundment. B—Upper impoundment facing downstream, showing incising right stream bank. Note the herbaceous floodplain showing previous impoundment water levels verified by inspection of historic aerial images. The floodplain has evidence of regular (e.g. 1-2 year frequency) flooding maintaining its shape, and so it falls within the bankfull channel defined in this paper. The active channel is incising into the sediments previously impounded within the bankfull

channel. C—The dam creating this impoundment, shown by arrow. Compare with Figure 2D, an actively maintained beaver dam. D—Close-up of dam showing lack of maintenance. Upper arrow points out beaver-chewed sticks marking top of dam. Lower arrow points out top of an earthen pipe, which formed following dam abandonment, draining water through the dam. E—Stranded beaver lodge in upper impoundment. Arrow points out lodge entrance that would have been submerged when the lodge was constructed.

Fig. 8. Mean active versus bankfull w:d suggests grouping of valley-wide ponds according to level of maintenance. A—VWP impoundments with maintained dams and a similar active and bankfull w:d, both of which are relatively high. B—impoundments with poorly maintained dams and much lower active w:d compared with bankfull, indicative of incising channels set within banks that were previously impounded and are still regularly flooded (e.g., Fig 7B).

Fig. 9. Scale-dependent classification system of a discontinuous river network focusing on beaver dams.

Tables

Table 1. Study reach properties.

Reach ID	Stream name	Reach class	Catchment size (km^2)	Active beaver	Stream order	Valley slope (%)	No. side channels	Riparian vegetation[1]
1.00	Fenton River	FF	51.6	--	4	1.0	0	f
1.01	Fenton River	FF	52.2	--	4	0.1	0	f
1.02	Fenton River	ICP	23.2	yes	3	0.7	1	h
1.03	Fenton River	FF	47.1	--	4	1.1	3	f
2.01	E Br Mount Hope	DD	7.5	no	3	0.3	3	f
2.02	E Br Mount Hope	FF	8.0	--	3	0.1	0	f
2.04	E Br Mount Hope	DD	5.9	no	3	3.7	3	f
2.06	E Br Mount Hope	FF	2.2	--	2	1.6	0	f,s
2.07	E Br Mount Hope	ICP	3.0	no	3	1.4	2	s
2.08	E Br Mount Hope	VWP	3.0	no	3	0.8	0	s
3.01	Charter Oak Brook	FF	0.2	--	1	4.8	0	f
4.010	Branch Brook	VWP	0.2	no	3	2.7	0	f
4.011	Branch Brook	FF	0.2	--	3	2.7	0	f
4.02	Branch Brook	DD	2.6	no	3	4.3	6	f
4.04	Branch Brook	FF	2.4	--	3	1.1	0	f,h
4.05	Branch Brook	ICP	2.4	no	2	1.0	1	h,f
4.06	Branch Brook	VWP	1.8	no	2	0.2	0	s,f
4.07	Branch Brook	VWP	1.8	no	2	0.8	0	h
4.10	Branch Brook	DD	4.3	yes	3	3.3	3	s,h
4.11	Branch Brook	VWP	4.3	no	3	0.2	0	s,f
4.12	Branch Brook	DD	7.2	no	3	1.5	6	h,f
4.14	French East	VWP	0.6	yes	1	0.1	0	s,f
4.15	French East	ICP	0.6	yes	1	0.7	0	h,s

4.16	Branch Brook	ICP	1.8	yes	2	0.4	1	h
4.17	French East	VWP	0.5	yes	1	0.1	0	f
4.18	Branch Brook	DD	4.7	yes	3	1.8	5	s,h
4.19	Branch Brook	VWP	4.7	yes	3	0.5	0	f,s
4.21	Branch Brook	VWP	1.8	no	2	0.2	0	f,s
4.22	Branch Brook	FF	2.5	--	3	4.0	0	f

Reach class abbreviations: FF—Free-flowing; ICP—In-channel beaver pond; DD—Downstream of beaver dam; VWP—Valley-wide beaver pond. Riparian vegetation abbreviations: f—forest; s—shrub; h—herbaceous. Note: [1] multiple vegetation types are provided in order of dominance.

Table 2. Channel shape morphology expressed as mean, minimum and maximum values of the cross-sections for each study reach.

Site ID	Reach class	Bankfull channel			Active channel		
		width (m)	depth (m)	w:d	width (m)	depth (m)	w:d
1.00	FF	N/A	N/A	N/A	12.8	0.50	28.1
					(10.7,14.9)	(0.30,0.80)	(15.9,35.1)
1.01	FF	14.2	1.20	12.0	13.9	0.80	16.9
		(12.1, 15.2)	(1.10, 1.20)	(10.6, 12.8)	(11.2, 15.2)	(0.80, 1.00)	(11.6, 19.5)
1.03	FF	14.9	0.9	17.9	13.5	0.4	33.9
		(13.9, 16.4)	(0.6, 1.0)	(14.6, 22.7)	(12.2, 15.6)	(0.3, 0.5)	(29.1, 40.2)
2.02	FF	11.9	0.7	18.2	10.7	0.4	34.5
		(11.2, 12.7)	(0.5, 0.8)	(13.8, 23.9)	(10.1, 11.1)	(0.2, 0.5)	(20.9, 51.5)
2.06	FF	14.9	0.4	34.6	2.8	0.2	15.6
		(14.9, 14.9)	(0.4, 0.4)	(34.6, 34.6)	(2.8, 2.8)	(0.2, 0.2)	(15.6, 15.6)
3.01	FF	4.7	0.2	30.3	N/A [1]	N/A [1]	N/A [1]
		(3.7, 5.6)	(0.1, 0.2)	(28.2, 32.4)			
4.011	FF	12.4	0.8	14.5	3.9	0.2	20.4
		(9.4, 18.3)	(0.7, 1.1)	(12.7, 17.4)	(3.0, 5.0)	(0.2, 0.2)	(20.0, 20.9)
4.04	FF	5.0	1.0	7.6	3.9	0.8	13.1
		(2.6, 7.9)	(0.6, 1.9)	(1.4, 14.3)	(2.2, 6.3)	(0.2, 1.7)	(1.3, 26.2)
4.22	FF	4.0	0.5	7.4	2.8	0.1	22.9
		(3.2, 4.8)	(0.4, 0.7)	(6.9, 7.9)	(1.9, 3.8)	(0.1, 0.2)	(18.7, 26.2)
2.01	DD	8.9	0.8	11.3	8.0	0.4	40.1
		(6.4, 10.5)	(0.5, 1.1)	(9.2, 14.3)	(5.8, 10.2)	(0.1, 0.8)	(13.4, 83.0)
2.04	DD	13.3	0.7	22.3	6.5	0.2	65.7
		(7.4, 22.8)	(0.5, 1.1)	(9.3, 46.5)	(4.1, 9.7)	(0.1, 0.2)	(18.9, 149.0)
4.02	DD	9.2	1.1	8.4	4.0	0.4	13.7

Site ID	Reach class	Bankfull channel			Active channel		
		width (m)	depth (m)	w:d	width (m)	depth (m)	w:d
		(7.3, 11.5)	(0.9, 1.7)	(6.8, 10.0)	(2.8, 5.0)	(0.2, 0.7)	(7.7, 17.2)
4.10	DD	4.0	0.5	8.3	2.4	0.1	29.4
		(3.7, 4.2)	(0.4, 0.6)	(6.6, 9.7)	(2.0, 2.8)	(0.1, 0.2)	(14.6, 40.6)
4.12	DD	14.9	0.8	20.2	7.7	0.4	19.6
		(13.8, 17.1)	(0.5, 1.0)	(16.7, 25.9)	(4.4, 10.9)	(0.2, 0.6)	(14.0, 23.8)
4.18	DD	30.8	0.6	43.2	5.4	0.2	29.5
		(5.0, 62)	(0.4, 0.8)	(13.6, 78.5)	(3.1, 9.0)	(0.1, 0.3)	(13.0, 51.3)
2.08	VWP	25.6	1.2	21.6	11.5	1.1	9.8
		(18.1, 34.8)	(0.9, 1.6)	(16.5, 26.7)	(4.8, 22.0)	(0.8, 1.4)	(6.0, 15.7)
4.010	VWP	13.9	0.9	15.4	9.7	0.7	13.4
		(9.6, 18.3)	(0.7, 1.1)	(13.4, 17.4)	(4.3, 15.3)	(0.6, 0.8)	(7.8, 19.6)
4.06	VWP	95.6	1.6	61.0	94.6	1.5	64.7
		(88.9, 101.6)	(1.4, 1.9)	(46.8, 68.5)	(88.8, 98.9)	(1.3, 1.8)	(49.3, 74.0)
4.07	VWP	12.3	0.8	16.0	4.5	0.3	16.4
		(10.8, 14.4)	(0.6, 0.9)	(11.5, 19.5)	(3.8, 5.6)	(0.2, 0.4)	(10.5, 23.7)
4.11	VWP	38.9	1.8	22.6	10.6	1.4	8.3
		(23.3, 49.7)	(1.4, 2.3)	(14.6, 31.3)	(4.5, 17.7)	(1.1, 1.9)	(3.8, 16.1)
4.14	VWP	85.9	1.5	58.9	84.0	1.4	64.6
		(51.2, 128.3)	(1.3, 1.8)	(28.0, 90.7)	(51.0, 123.0)	(1.2, 1.7)	(30.6, 100.4)
4.17	VWP	99.2	1.3	79.4	83.8	1.1	79.1
		(84.2, 114.2)	(1.3, 1.3)	(67.4, 91.4)	(77.5, 90.0)	(1.0, 1.1)	(69.5, 88.7)
4.19	VWP	80.4	1.5	54.0	13.1	1.3	10.1
		(61.3, 96.8)	(1.3, 1.7)	(37.2, 74.5)	(7.2, 22.2)	(1.1, 1.5)	(5.5, 15.3)
4.21	VWP	75.5	1.9	46.1	62.7	1.7	46.3
		(57, 96.2)	(1.2, 2.5)	(29.1, 79.5)	(41.5, 75.1)	(0.9, 2.5)	(24.1, 85.8)
1.02	ICP	7.7	0.9	8.4	7.7	0.6	12.3

Site ID	Reach class	Bankfull channel			Active channel		
		width (m)	depth (m)	w:d	width (m)	depth (m)	w:d
		(7.2, 8.4)	(0.8, 1.0)	(8.0, 8.8)	(7.2, 8.4)	(0.5, 0.8)	(10.9, 14.2)
2.07	ICP	4.8	0.4	10.2	2.1	0.1	27.6
		(2.5, 7.0)	(0.4, 0.5)	(6.2, 14.2)	(1.0, 3.3)	(0.0, 0.2)	(16.7, 38.4)
4.05	ICP	6.1	0.6	10.2	3.0	0.1	24.5
		(5.1, 7.4)	(0.4, 0.8)	(8.3, 12.8)	(2.4, 4.0)	(0.1, 0.2)	(15.7, 33.0)
4.15	ICP	12.3	1.0	13.3	9.6	0.5	17.5
		(8.9, 17.2)	(0.9, 1.1)	(8.4, 20.0)	(6.6, 14.8)	(0.4, 0.6)	(13.7, 24.0)
4.16	ICP	12.6	0.9	13.6	8.1	0.5	16.1
		(9, 18.3)	(0.6, 1.2)	(9.5, 15.7)	(7.9, 8.2)	(0.4, 0.6)	(14.3, 19.5)

Values in parentheses are minimum and maximum values for each reach. See text for definition of active channel. See Table 1 for reach class abbreviations. Note: [1] Intermittent stream with no active channel

Table 3. Transect geometry along the channel for the four reach classes.

Stat	Upstream				Central				Downstream			
	FF	DD	VWP	ICP	FF	DD	VWP	ICP	FF	DD	VWP	ICP
Bankfull w:d												
	ANOVA: F(3,22)=7.7, **p=0.001**				ANOVA: F(3,22)=5.2, **p=0.007**				ANOVA: F(3,20)=4.9,**p=0.01**			
mean	14.9	15.9	<u>**56.4**</u>	<u>**9.0**</u>	18.0	<u>11.7</u>	<u>**36.5**</u>	<u>10.8</u>	12.4	19.1	<u>**34.3**</u>	14.3
σ	5.9	<u>**15.6**</u>	<u>**34.5**</u>	<u>**1.9**</u>	11.2	<u>**3.0**</u>	<u>**22.3**</u>	<u>**3.6**</u>	4.5	<u>**11.6**</u>	<u>**16.5**</u>	4.7
n	7	6	8	5	8	6	7	5	6	6	8	4
Active w:d												
	ANOVA: F(3,23)=1.14, p=0.35				ANOVA: F(3,23)=0.46, p=0.71				ANOVA: F(3,22)=1.31,p=0.29			
mean	21.4	41.7	<u>48.8</u>	22.3	25.2	19.7	25.9	<u>15.6</u>	19.7	37.0	30.0	19.4
σ	9.0	<u>**53.1**</u>	<u>**41.4**</u>	12.5	15.9	<u>**6.1**</u>	<u>27.4</u>	<u>**3.1**</u>	10.7	27.6	19.7	5.8
n	8	6	8	5	8	6	8	5	8	6	8	4

Bold and underlined values—significantly different when compared with FF reach class, p<0.05. Underlined values not bold—p<0.1 when compared with FF reach class.

Table 4. Distinguishing features of the three beaver-modified reach types in comparison with free-flowing channel reaches.

Reach class	Shape characteristics	Sediment characteristics	Inferred processes
Downstream of beaver dam	Located in steep valleys. Multi-thread channel, which converges to single-thread channel downstream. High variability of channel shape along a reach. High variability of channel shape between reaches, especially closest to the beaver dam. Main channel thread similar in shape to a free-flowing channel. .	Similar to free-flowing channel or slightly finer, despite an expectation of coarser sediments due to steeper slopes.	Excavation of new channels downstream of beaver dam due to channel avulsion caused by the dam. Possible deposition of pockets of fine sediment during recession of high flows that had mobilized upstream impounded sediments.
Valley-wide beaver pond	Located in shallower grade valleys. Greater channel widths and depths, and greater w:d ratios compared with the free-flowing channel Dominant discharge w:d >= active w:d. Extremely high variability in channel shape between reaches.	Primarily organic sediments, including undecomposed roots and wood. Loss of sediment in old ponds where the beaver dam is abandoned and leaky.	Deposition of fine sediments and organic material in ponds of actively maintained dams and in all ponds during lower flows. Mobilization of impounded sediments during flood flows. Erosion of impounded sediments during high flows in ponds with abandoned dams.

Reach class	Shape characteristics	Sediment characteristics	Inferred processes
In-channel beaver pond	Located in shallower grade valleys, but generally steeper than valley-wide beaver ponds. Lower bankfull w:d and narrower channel widths in the upper reaches. Lower variability in w:d.	A mixture of coarse and fine sediments.	Patchy erosion and deposition, with patches varying across space and time. Deposition occurs while dams are intact. Deposited sediments are fine and highly organic. Erosion occurs when dams fail. Erosion generates channel incision into previously impounded soft sediments. Densely vegetated banks resist erosion. Eroded material is transported out of the reach.

Figure 1

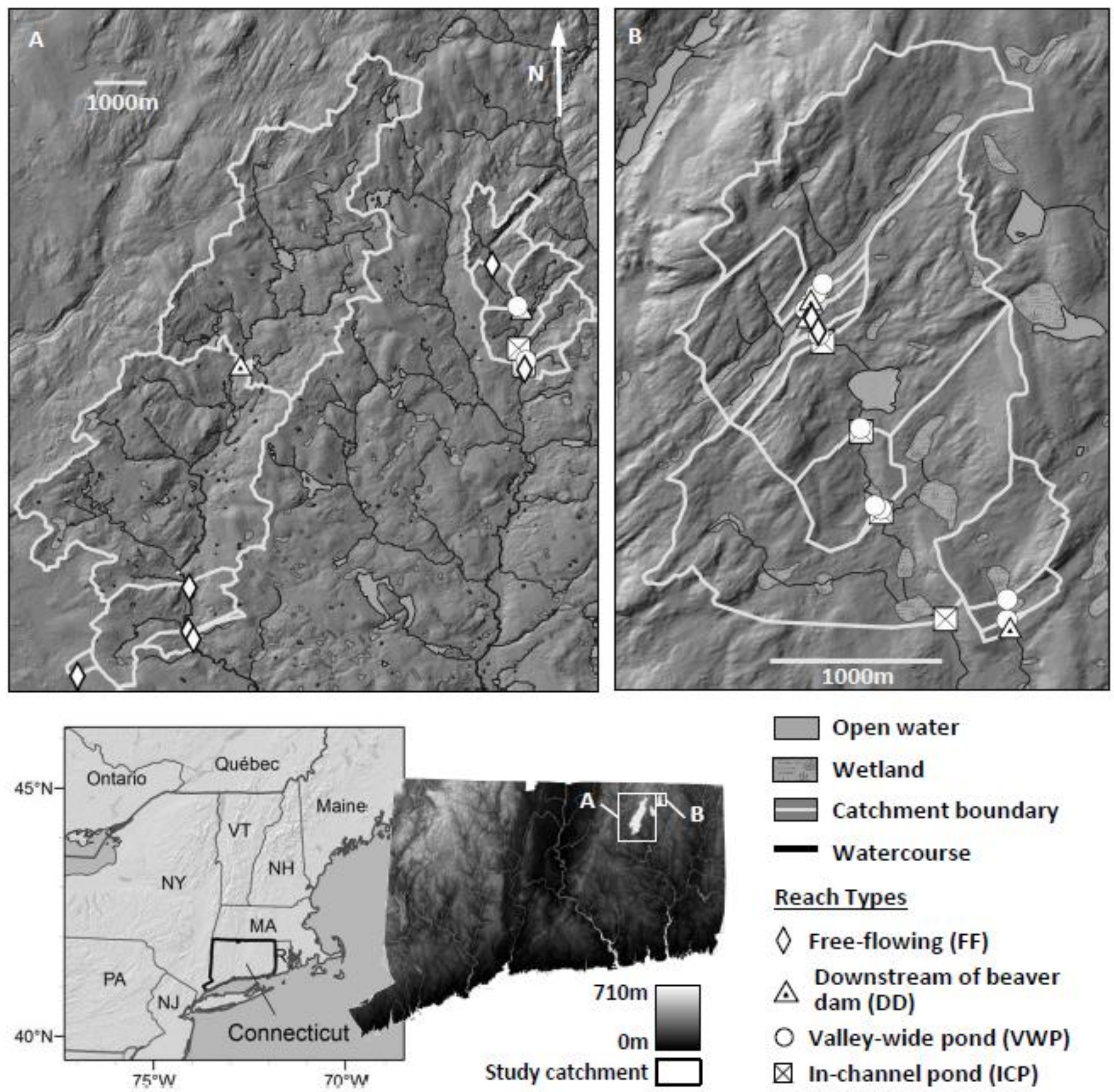

A
1000m
N
B
1000m
Ontario
Québec
45°N
40°N
Maine
VT
NH
NY
MA
RI
PA
NJ
Connecticut
75°W
70°W
A
B
710m
0m
Study catchment
Open water
Wetland
Catchment boundary
Watercourse
Reach Types
Free-flowing (FF)
Downstream of beaver dam (DD)
Valley-wide pond (VWP)
In-channel pond (ICP)

Figure 2

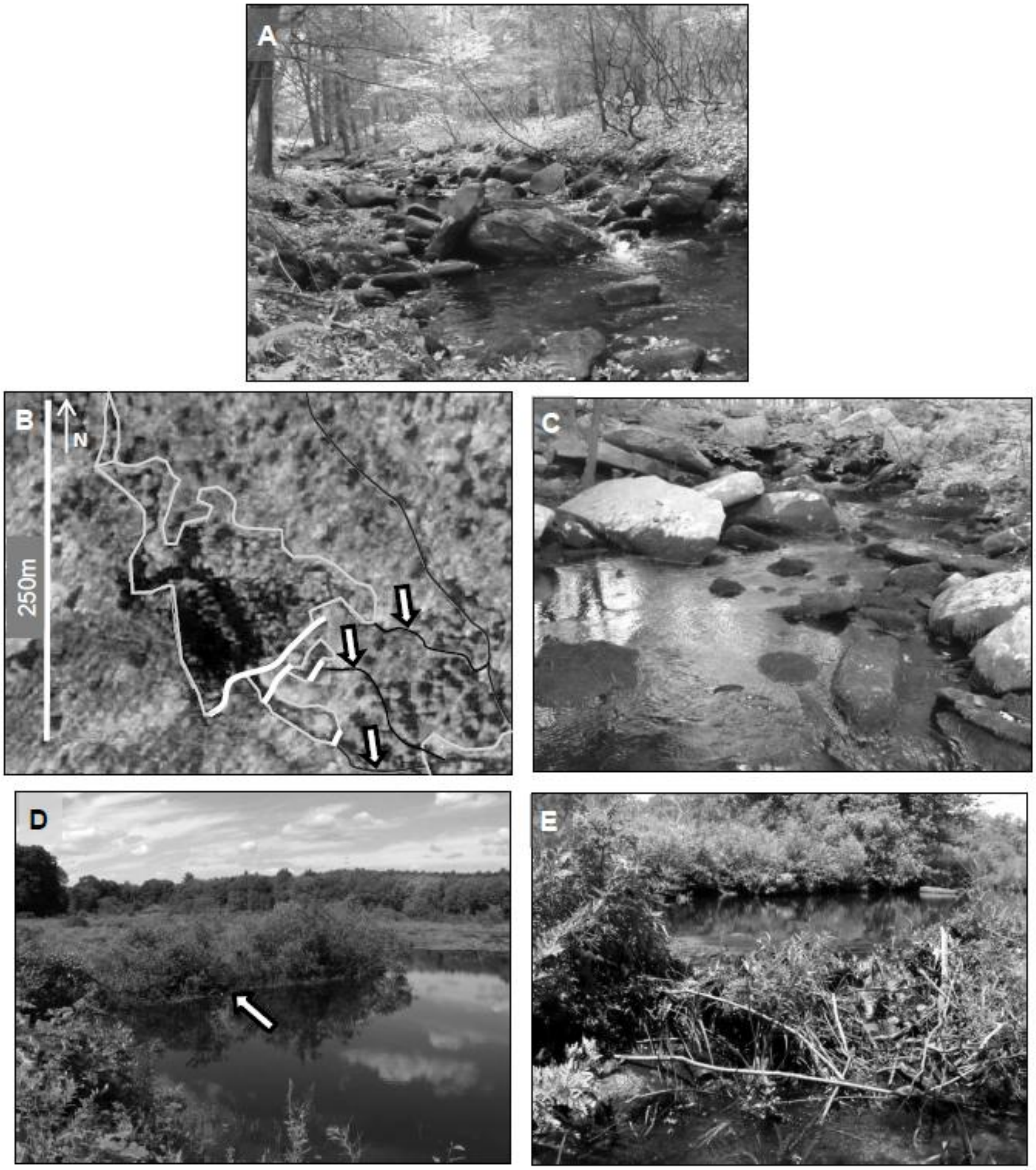


Figure 3

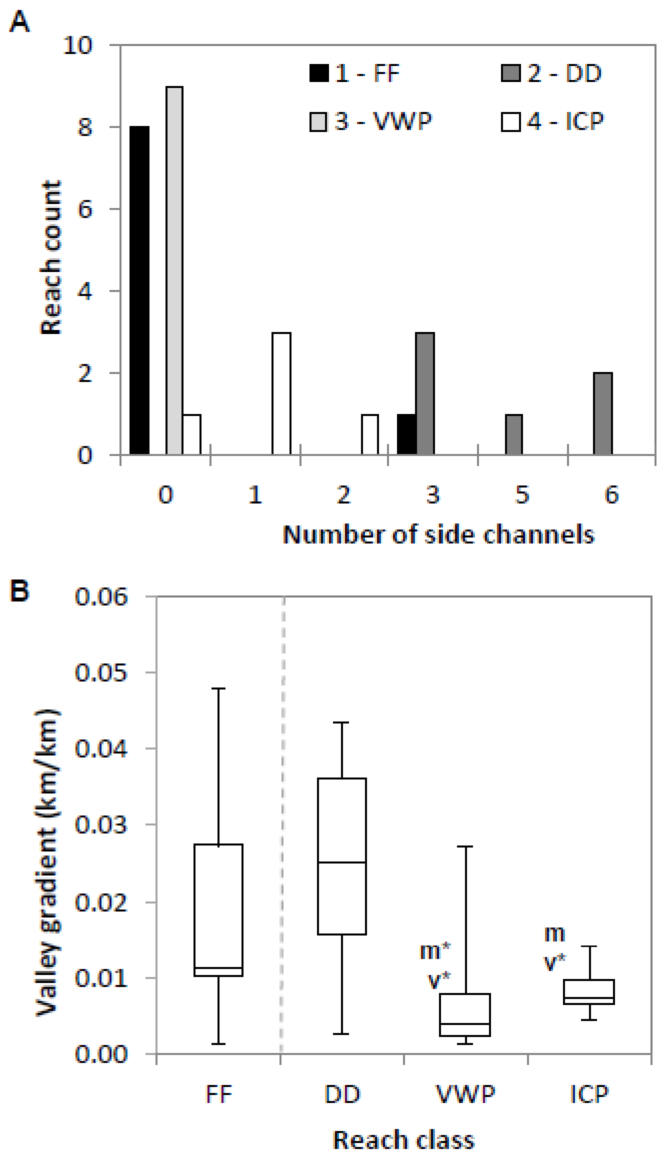

A
10
8
6
4
2
0
Reach count
1 - FF
2 - DD
3 - VWP
4 - ICP
0
1
2
3
5
6
Number of side channels
B
0.06
0.05
0.04
0.03
0.02
0.01
0.00
Valley gradient (km/km)
m*
v*
m
v*
FF
DD
VWP
ICP
Reach class

Figure 4

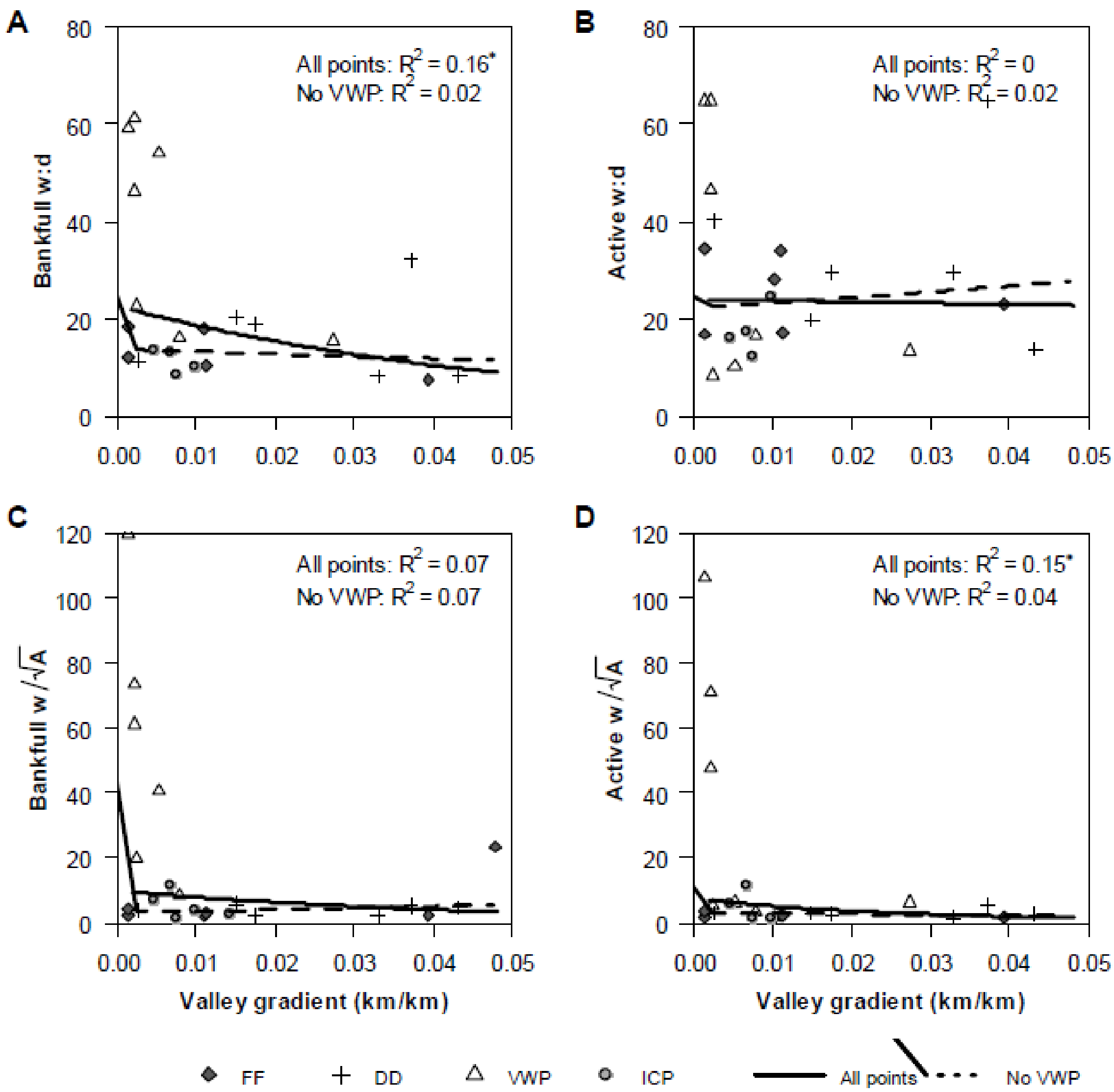

A
B
C
D
All points: R^2 = 0.16*
No VWP: R^2 = 0.02
All points: R^2 = 0
No VWP: R^2 = 0.02
All points: R^2 = 0.07
No VWP: R^2 = 0.07
All points: R^2 = 0.15*
No VWP: R^2 = 0.04
Bankfull w:d
Active w:d
Bankfull w / √A
Active w / √A
Valley gradient (km/km)
FF
DD
VWP
ICP
All points
No VWP

Figure 5

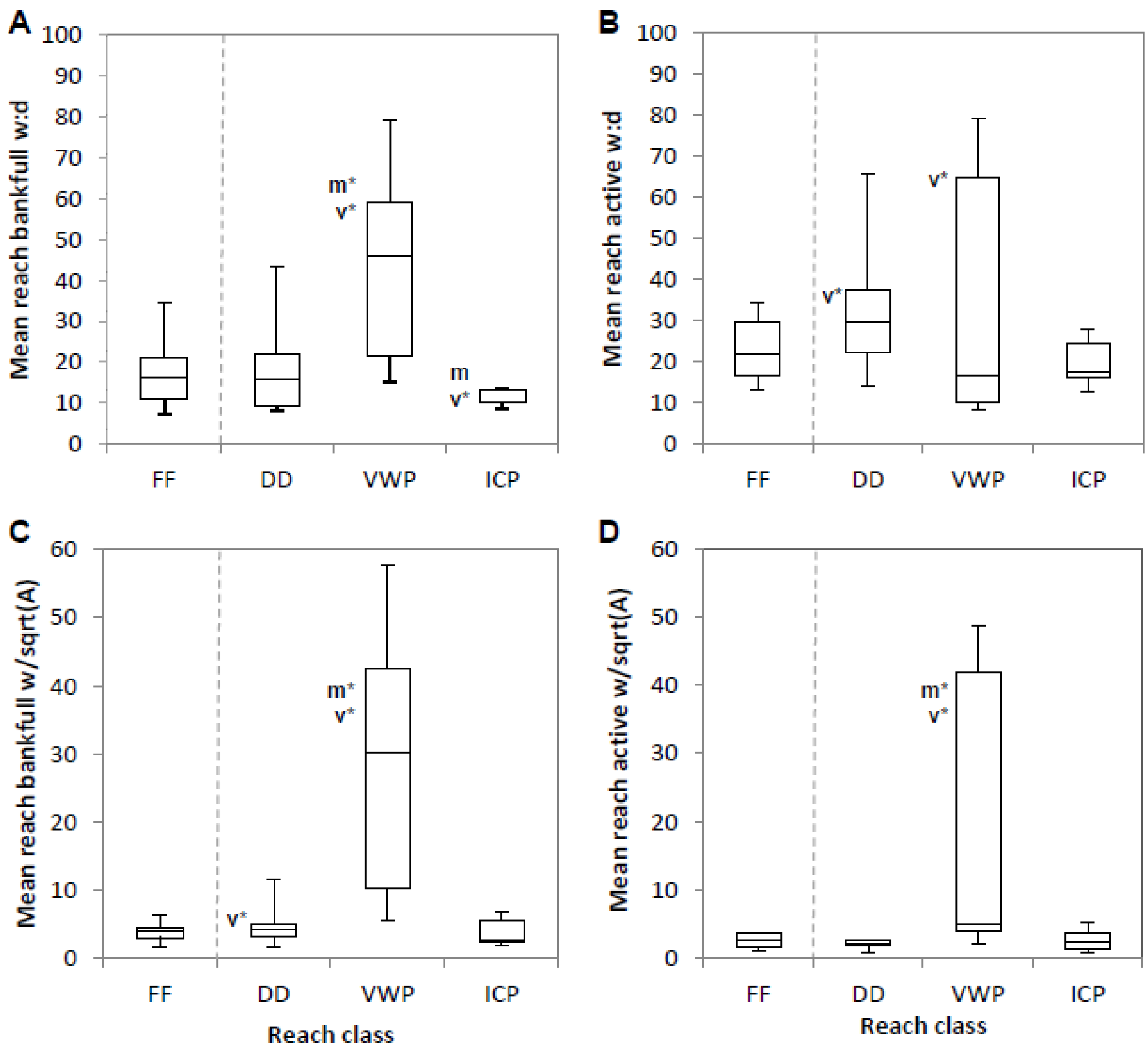

A
Mean reach bankfull w:d
m*
v*
m
v*
FF
DD
VWP
ICP
B
Mean reach active w:d
v*
v*
C
Mean reach bankfull w/sqrt(A)
v*
m*
v*
Reach class
D
Mean reach active w/sqrt(A)
m*
v*

Figure 6

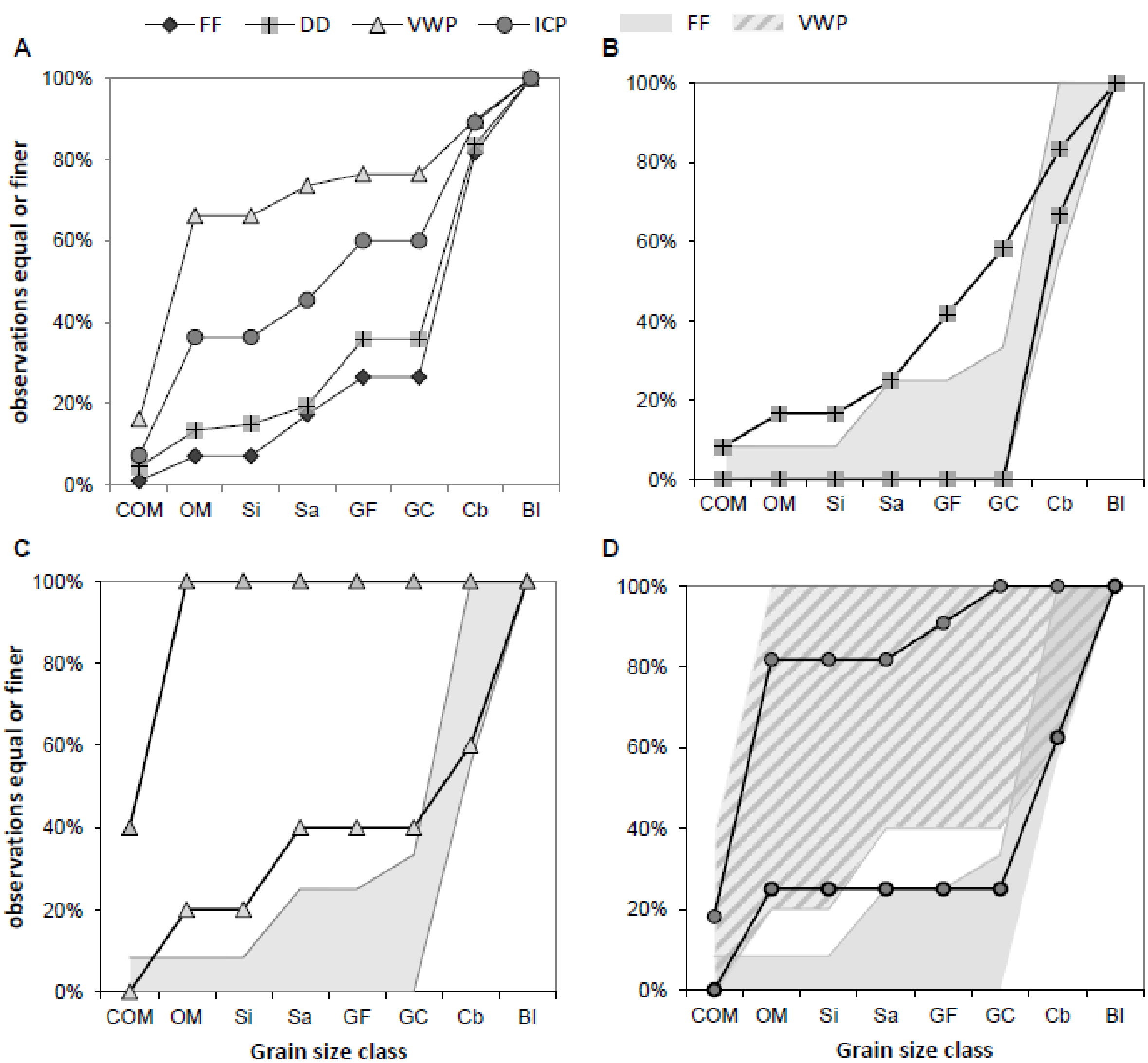

FF
DD
VWP
ICP
FF
VWP
A
B
C
D
100%
80%
60%
40%
20%
0%
observations equal or finer
COM
OM
Si
Sa
GF
GC
Cb
Bl
Grain size class

Figure 7 (A & B)

Figure 7 C-E

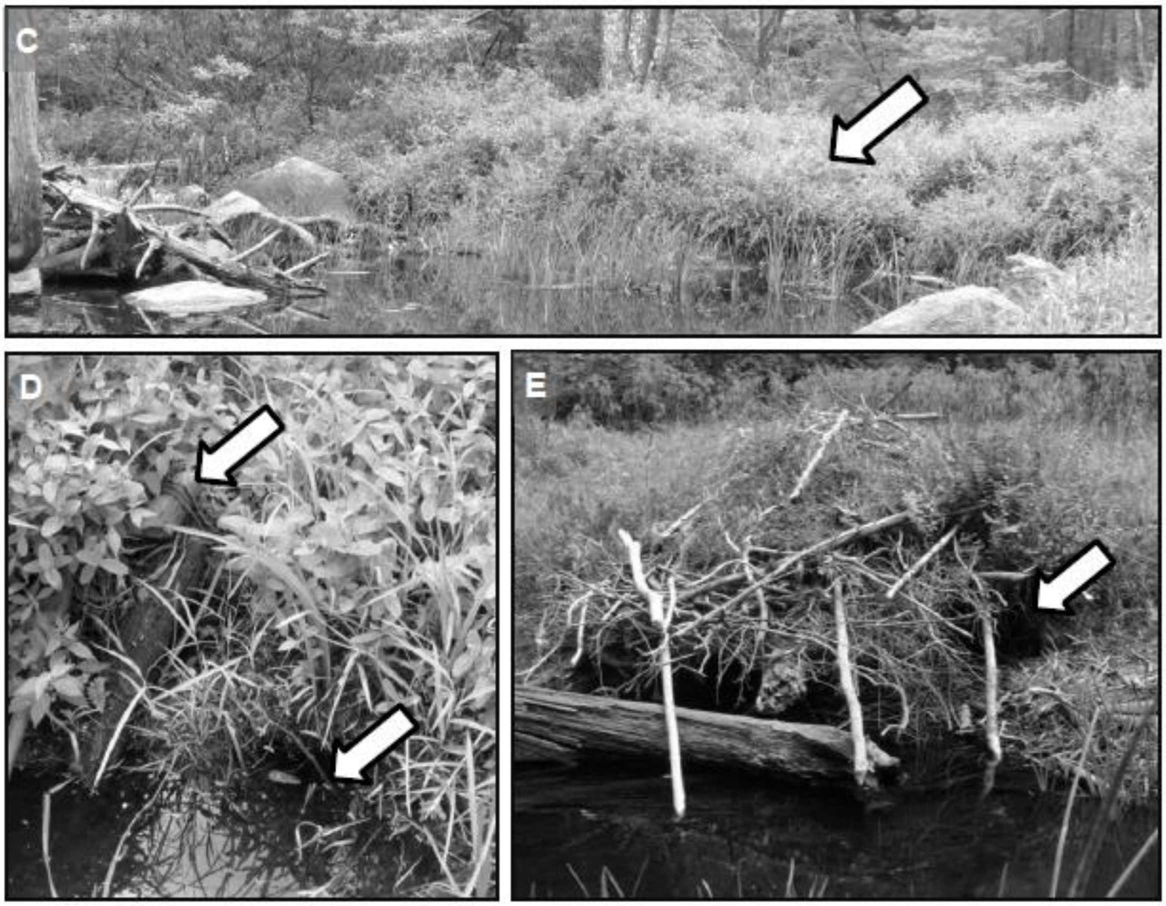
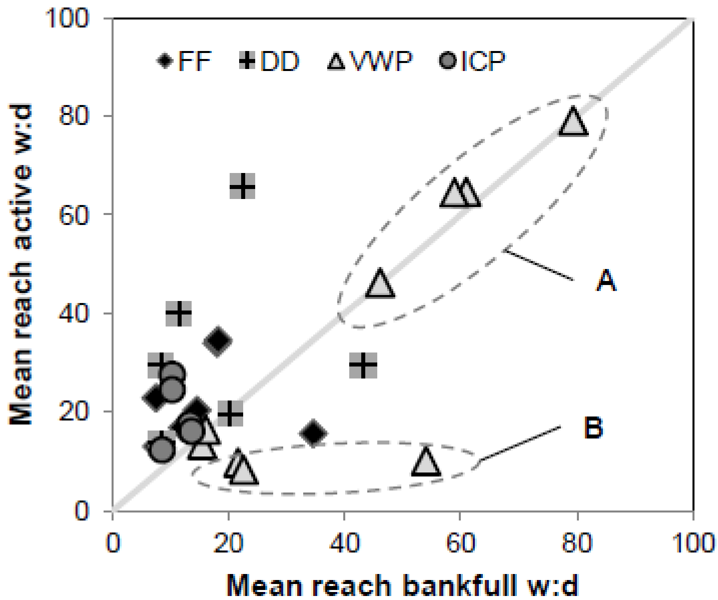


Figure 8



FF
DD
VWP
ICP
A
B
Mean reach active w:d
Mean reach bankfull w:d
0
20
40
60
80
100

Figure 9

Scale	**Classification**		
Network (10^3m, 10^5-10^6 yr)		Discontinuous network (colonized by beavers) ↓	
Segment (10^2m, 10^2-10^4 yr)	Free-flowing segments ↓	Impounded segments (beaver ponds) ↓	Meadow segments (beaver meadows) ↓
Reach (10^1-10^2m, 10^1-10^4 yr)	• Existing reach classification systems • Downstream of beaver dams	• Valley-wide beaver ponds (potential split between ponds formed by active vs. abandoned dams) • In-channel beaver ponds	*Requires study*

Highlights

- Beaver dams are small but frequent in time and space.
- We compared shape and substrate of four reach classes in networks with beavers.
- Bankfull w:d and width/square root catchment area are distinct between classes.
- Distinct channel shape and substrate suggests decoupled processes between classes.
- Proposed classification includes free-flowing, impounded, and meadow categories.