Do abandoned beaver dams act as natural water filters?

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Abstract

Through building dams, *Castor canadensis*, the North American beaver, engineers stream ecosystems into spatial and temporal mosaics composed of stagnant ponds and free-flowing stream channels. The landscape heterogeneity created by beavers is linked to the ecosystem service of nitrate reduction in stream water, which entails reduced nitrate loading to estuarine and coastal waters. This research examines the effects of a beaver-dominated landscape upon nutrient uptake in Cart Creek, a forested, first-order stream in eastern Massachusetts. The organic matter content and denitrification potential of sediments taken from beaver ponds, dams, and sections of the stream channel were compared. Nitrate concentrations were compared along a 1 km downstream transect, as well as above and below individual dams. Nutrient pulse additions were performed at two abandoned dams to test the hypothesis that permeable structures of decaying wood act as trickle filters, in which nitrate is removed from the water as it passes through the dams. Sediment characteristics and nitrate concentrations along a downstream transect did not differ substantially, suggesting that Cart Creek did not reflect the level of heterogeneity expected of a beaver-impounded stream. Nutrient pulse additions determined that the abandoned dams did not act as trickle filters. However, a trend of nutrient uptake immediately downstream of the dams indicates that the presence of dams does influence nutrient processing variability within a stream reach.

Key words and phrases: beaver, *Castor canadensis*, ecosystem engineer, landscape alterations, habitat heterogeneity, beaver dams, nutrient cycling, nitrate uptake, eutrophication, ecosystem service, impoundment, nutrient pulse addition

Introduction

For the first time in nearly four centuries, people are experiencing the effects of living alongside flourishing populations of an ecosystem engineer—*Castor canadensis*, or the North American beaver. Beavers once inhabited almost every aquatic ecosystem between northern Mexico and the arctic tundra. Trapping for the fur trade sparked rapid population decline in the 17th century, and by the 20th
century, the North American beaver was virtually extinct (Naiman et al., 1988). Due to trapping restrictions, relative absence of predators, and restoration of wetland habitat, beavers have recently begun repopulating sections of their former range, including eastern Massachusetts.

The presence of beavers is marked by their unmistakable alterations to the landscape. Beavers gnaw trees to chop them down, build dams across streams, and create ponds and wetlands by impounding water behind dams. These activities transform a homogenous habitat of free-flowing stream into a heterogeneous mosaic of ponds and stream channel sections (Naiman et al., 1988). Beaver-impounded streams are temporal mosaics in addition to spatial mosaics, as the density of dams in a stream and the current maintenance status of the dams constantly shift depending on colonization activities. Many landowners consider beavers to be a nuisance, owing to the felling of ornamental trees or the flooding of their properties. However, people do not necessarily realize that the engineering activities of beavers may be providing important ecosystem services.

Most of our current limnological knowledge is based upon stream ecosystems that lack the degree of influence incurred by beavers in the pre-17th century landscape (Naiman et al., 1988). As beaver populations recover, we are beginning to understand the nature and scope of beavers’ ecosystem alterations. The act of building dams creates and maintains wetlands, alters nutrient cycling and decomposition dynamics within stream channels, changes the structure of the riparian zone, affects the nature of materials transported downstream, and influences plant and animal community composition (Naiman et al., 1988).

These ecosystem alterations certainly intersect with human-induced alterations to the environment. Anthropogenic nutrient loading is of particular concern in eastern Massachusetts, where the nutrient loads in streams are deposited into estuarine and coastal waters. Excess loading of nutrients such as nitrate causes eutrophication, which lowers biodiversity and threatens fisheries production. Research has shown that streams with beaver dams have reduced nitrate concentrations, indicating that beavers may be providing the invaluable service of reducing nitrate loading to estuaries.
Several studies have addressed how the retention of water and sediment in beaver dam impoundments affects nitrogen cycling dynamics within streams. Impoundments sequester nitrogen for longer time periods than free-flowing sections of stream, thereby decreasing nutrient spiraling length and increasing ecosystem retention and processing efficiency (Naiman & Melillo, 1984). Nitrogen turns over upwards of 20 times more slowly in beaver ponds than in riffles, resulting in ponds holding 37 times more nitrogen (Naiman & Melillo, 1984). A study of two streams on the Appalachian Plateau identified beaver impoundments as sinks of nitrate and sources of ammonium, suggesting that nitrate is reduced to ammonium in impoundments (Margolis et al., 2001). This study showed that nitrate concentrations below individual dams were lower than nitrate concentrations above dams on a second-order stream. A study in central New York found that nitrate concentrations were greatly reduced downstream along the length of a beaver-impounded stream (Klotz, 2010). Nitrate reduction was attributed to denitrification occurring in beaver impoundments. Increased water residence times and the respiration of accumulated organic matter in the impoundments create an anaerobic environment, where denitrification is likely to occur.

In addition to the denitrification supported by increased nitrogen residence time in beaver ponds, it is possible that the structural components of dams themselves help to create conditions necessary for denitrification. Decaying wood serves as a substrate for microorganisms that perform denitrification. Experimental permeable reaction barriers made of woodchips have been installed at Waquoit Bay and the Child’s River on Cape Cod, with the assumption that the woodchips will support denitrifying microorganisms (personal communications, Vallino and Foreman, 2015). The goal of the barriers is to reduce nitrogen loading to the estuary. I hypothesized that the wood in beaver dams may function similarly to these permeable reaction barriers. Most beaver dams are maintained by the packing together of fresh mud and sticks for less than 10 years, and are then abandoned (Burchsted, 2014). Abandoned beaver dams may be most likely to support denitrification. They are more permeable than actively maintained dams in that
water is able to trickle through the crumbling structure of wood and sediment, bringing the water into contact with denitrifying microbial communities.

I studied the effects of beavers as ecosystem engineers at Cart Creek, a first-order stream in eastern Massachusetts that contains several active and abandoned beaver dams. I characterized the overall landscape alterations caused by beavers and sought to understand the effects of dams and impoundments on nutrient cycling in the stream. I tested the hypothesis that sediments taken from different sections within a reach of stream would have different capacities for potential denitrification, expecting that sediments from within ponds and the insides of abandoned dams would have the highest denitrification potential. Additionally, I tested the hypotheses that nitrate concentrations are reduced along a downstream transect (Klotz, 2010) and from a pond to the outflow at the bottom of a dam (Margolis et al. 2001). Finally, I tested the hypothesis that abandoned beaver dams act as trickle filters, in which nitrate is removed from water as it passes through the dam.

**Methods**

In addition to characterizing ecosystem alterations caused by beavers, my research consisted of three main experiments. I set up a sediment incubation to measure denitrification potential via nitrate drawdown, analyzed nutrient concentrations taken from samples above and below dams along a downstream transect, and performed nutrient pulse additions at two abandoned dams to test the trickle filter hypothesis.

**Study Sites**

I conducted my experiments at Cart Creek, a first-order stream in the Martin Burns Wildlife Management Area in Newbury, MA. Cart Creek is a tributary to the Parker River, which empties into Plum Island Estuary. I studied a reach of stream containing six dams, two of which were abandoned beaver dams, two of which were rock dams composed of rocks from old stone walls, one of which was an active beaver dam, and one of which was a large beaver dam recently breached by the building of a road (Table 1). Data were collected on November 10-12, 18-20, and 23-
24, 2015. Water levels were low in November. Flow in the upstream portions of the reach was barely measurable, and flow in the downstream portion near dam 6 was estimated at 5-10 L/s. Cart Creek originates in a wetland adjacent to a heavily traveled interstate highway. Dams 1 and 2 parallel a dirt road with very light traffic. The management area is used recreationally for hunting.

**Characterization of ecosystem alterations**

I categorized dams as “active” or “abandoned” based on the permeability of the dam. Active dams were obviously impermeable. Active dams and recently breached dams created notably larger impoundments than abandoned dams. I measured the size of impoundments through aerial photographs or with a measuring tape, depending on size. I measured the change in hydraulic head at each dam by creating a syphon with a plastic hose, and measuring the height at which water flowed out of the hose. Where possible, I measured stream flow above and below each dam with a current meter, but flows were barely detectable in most locations.

**Sediment incubation to measure potential denitrification**

At dam 2, I collected sediment from five locations: the impoundment, within the macro-pore opening on the downstream side of the dam, 0.5 m downstream of the dam, 6 m downstream of the dam, and 20 m downstream of the dam. At each site, I filled five 60- mL syringe corers with the top 2-3 cm of sediment, and homogenized the sediments within plastic bags. I took two replicates per location. After sampling, I set up a 4-day time course in which sediment from each site was incubated in an anaerobic vial with added sodium nitrate. I weighed out 2 wet grams of sediment from each site into 160-mL serum vials. I used 3 L of stream water to make a .01 M sodium nitrate solution and added 50 mL of solution to each vial. I sealed the vials with rubber gaskets and flushed the headspace of the vial with N\textsubscript{2} gas. I designated two replicates from each site to filter 20 mL of water at time zero, 24 hours, 48 hours, 72 hours and 96 hours. I analyzed the filtered samples for ammonium and nitrate concentrations using modified protocol from Wood et al.
(1967) and Griess (1879). For nitrate concentrations, I used an automated flow injection analyzer, the Lachat ® QuickChem 8500 Series 2.

I measured weights and weight percent of carbon and nitrogen in the sediment samples using the Thermo Scientific ® CN Analyzer: Model Flash 2000.

**Analysis of nutrient concentrations along a downstream transect**

I collected water samples above and below each dam to analyze for nitrate, ammonium and phosphate concentrations. I filtered samples in the field using Swinnex filter holders and 25 mm GF/F filters. After sampling, I followed the same colorimetric analysis procedures cited above to measure nitrate and ammonium concentrations in the samples. I used modified protocol from Murphy & Riley (1962) to measure phosphate concentrations.

**Nutrient pulse addition**

I performed nutrient pulse additions at dams 4 and 2, respectively, so as to add nutrients to the downstream site first. The objectives of these additions were to add to the pond a biologically active form of nitrate plus a conservative tracer to track downstream movement of the pulse, mix the additives within the pond, release the additives through the dam and track downstream movement of the pulse by measuring conductivity in the stream channel.

In order to raise the background nitrate levels to a desired concentration of 20 μM, approximately five times the background level, I surveyed each impoundment to calculate an area that contained approximately 100 L³ of water. I staked down a seine net weighted with rocks and covered in plastic across the impoundment to partition off the 100-L³ section. I covered the upstream face of the dam with a sheet of plastic, to keep the water from flowing through before the additive was mixed. I dissolved 1 L of .025 M sodium nitrate into a 1-L carboy of water from the impoundment along with 4-5 kg of sodium chloride. The sodium chloride addition was enough to raise the conductivity to approximately 5.6 mS/cm, about 25 times the background conductivity. I used road salt as a source of sodium chloride. I divided the carboy into three sprinkling cans, sprinkled the solution
throughout the impoundment, and mixed the water in the impoundment with a canoe paddle. I attempted to minimize disturbance of the sediment, but this was difficult given that both impoundments was less than 0.5 m deep in some places. At dam 4, I completely sealed off the impoundment from bank to bank so as to prevent upstream flow from entering the mixing area. At dam 2, I left a few inches of space between the barrier and the river left bank; the small amount of inflow seemed to help the water in the 100-L section to mix more thoroughly.

After allowing the additive a few minutes to mix throughout the pond, I sampled water from the pond. I then removed the plastic sheet covering the dam and sampled water from just below the dam (approximately 0.5 m), 2 m, 4 m, 8 m, 16 m and 32 m downstream of the dam. I continued this process in a time course, sampling in 15-minute intervals for one hour, then waited 20-30 minutes to take the last sample. To track the flow of the pulse, I kept Hydrolabs® stationed at 8 m and 16 m downstream to measure conductivity. I recorded conductivity values approximately every 5 minutes. At dam 4, the time course lasted 90 minutes. I took samples only at 16 m and 32 m at the last time point, because conductivity values indicated that the pulse had moved beyond the upstream stations. To ensure that all samples were captured in quick succession, I used plastic containers to scoop water from each station, then returned to filter 20 mL of water from each container into an acid-washed scintillation vial. At dam 2, I collected water samples to only 16 m downstream, because the channel emptied into the impoundment from dam 3 shortly thereafter. The time course lasted 80 minutes at dam 2. I only sampled from 8 m and 16 m downstream at the last time point.

At each dam, I placed the bottom of a 50-gallon drum upside down in the impoundment. At dam 4, I took a water sample from the tank at 60 and 90 minutes, assuming that the first sample I took in the impoundment would represent a sample taken from the tank. At dam 2, I took a sample from the tank at 10 min and 68 min. I sampled from the tank as a means of measuring nitrate uptake in a fixed area from which the water would not be moving out of the pond, and presumably with no other water inputs. I knew that chloride concentrations in the tank would remain
constant, and could assume that any changes in nitrate concentrations would reflect benthic uptake.

**Nutrient pulse addition analysis**

I analyzed samples from the nutrient pulse additions for nitrate concentrations using the adapted protocol from Wood *et al.* (1967) and Griess (1879), and the Lachat® QuickChem 8500 Series 2. I analyzed samples for chloride concentrations using the Thermo Scientific® Dionex DX-120 ion chromatograph. I calculated the ratios of nitrate to chloride, assuming that chloride could only be diluted and would not be generated in the stream. Thus, a decrease in the ratio of nitrate to chloride corresponded to nitrate removal, and an increase in the ratio corresponded to nitrification. Reductions in successive nitrate peaks among downstream stations can be accounted for by dilution, but because nitrate is biologically active, biological uptake and production processes also affect concentrations. Changes in the ratios of nitrate to chloride at the time the pulse hit each station indicate whether nitrate uptake or production occurred between stations.

I planned to correct nitrate concentrations at each site for background by subtracting the time zero concentration from that site from the rest of the time points. However, background concentrations were similar enough to those of the other time points that they brought nitrate concentrations too close to zero for the nitrate to chloride ratio to be accurate, so I omitted this correction from my analysis. I omitted background corrections for chloride as well, as background levels were so low that differences were negligible.

I estimated the mass of nitrate removed between 0.5 m and 4 m at dam 2, by calculating the area under the nitrate curves from each of these sites, finding the difference, and multiplying the difference by discharge. I found discharge by estimating the flow rate at this part of the reach based on distance traveled and travel time, and multiplying flow rate by the cross-sectional area of the channel.
Results

*Sediment incubation results*

Nitrate drawdown occurred by the end of the incubation in all of the sediment samples. Some of the replicates showed an increase in nitrate at some point during the time course, but all final concentrations were lower than initial concentrations (Figure 4, Figure 5). The sediments from inside of the dam removed the greatest percentage of total initial nitrate concentration, followed by sediments from 0.5 m downstream and from 20 m downstream (Figure 6). The highest daily rate of nitrate drawdown occurred 20 m downstream, followed by within the dam and just below the dam (Figure 7). The pond had a slightly higher daily rate of nitrate drawdown and removed a slightly larger amount of total nitrate than the sediments from 6 m downstream (Figure 7).

The drawdown of nitrate observed in the sediment incubations represents the potential of microbial communities in the sediments to remove nitrate. The high average percentage of nitrate removed by the sediments from the dam, 0.5 m and 20 m downstream indicate that the microbes living in these sediments are effective at removing nitrate. Taking standard error into consideration, both the percentage removed and the daily removal rate of the dam sediments are essentially the same as the sediments from 0.5 m downstream (Figure 6, Figure 7). This indicates that microbial communities are similar inside of the dam and directly below the dam, possibly because sediment from the dam falls or seeps out of the dam and builds up directly downstream.

Mineralization of ammonium occurred in the sediments from the pond, the dam, and 20 m downstream. Mineralization rates ranged from 1-5 μM/day, with the downstream sediment having a slightly higher rate than the dam, and the pond a considerably lower rate than the dam (Figure 8).

Carbon to nitrogen (C:N) ratios were highest in the dam and at 6 m downstream (Table 2). The lowest C:N ratio was found in the pond. The highest percentage of organic matter including carbon and nitrogen was found 20 m downstream, and the lowest was found in the dam. Ratios and percentages were
overall similar, though, illustrating relative uniformity of sediment types throughout the reach.

*Nutrient concentrations along a downstream transect*

Nitrate concentrations in Cart Creek were low, between 1-5 μM (Figure 2). Concentrations increased along a downstream transect until dam 6, where they dropped. Differences between most dams were slight, except for the drop between dam 5 and dam 6. Nitrate concentrations were reduced within sites at half of the sites, but differences within most dams were slight (Figure 2). Dam 4 showed the biggest reduction from above to below the dam, at 34% (Table 3). Dam 3 showed a large difference as well, but concentrations were higher above the dam than below the dam. The increase in nitrate concentrations between dams 1-5 reflects slight nitrate accumulation moving downstream, perhaps from groundwater inputs. Dam 6 was considerably farther downstream than all of the other dams, so the low concentrations seen at dam 6 may reflect spatial variation in any groundwater nitrate inputs (Figure 3).

Ammonium concentrations were below the detectable limit. Phosphate concentrations were less than 1 μM at all of the dams, so differences between and within dam sites were negligible (Figure 3). Freshwater systems tend to be phosphorous-limited, so low phosphate concentrations were to be expected. Low ammonium concentrations indicate that conditions in the stream are generally not favorable for mineralization or dissimilatory nitrogen reduction to ammonia.

*Nutrient pulse addition*

Conductivity peaks show the transit of the pulse addition through the system. At both dams, conductivity of the stream peaked at 8 m before it peaked at 16 m (Figure 9, Figure 10). The peaks occurred earlier and were higher in dam 4 than in dam 2. Peaks indicate that the travel time of the pulse at dam 4 between 8 m and 16 m was 10 minutes. The travel time between peaks at dam 2 was 19 minutes. The flow rate at dam 2 was estimated to be 0.01 m/s, too low to be accurately measured with a current meter.
Nitrate concentrations at the different stations during the time course also indicate that the addition moved through the systems as a pulse. At dam 4, the initial concentration of nitrate reached in the pond after mixing in the additive was 10.7 μM (Figure 11). The peak nitrate concentrations for stations 0.5 m, 2 m, 4 m and 8 m occurred at 15 minutes. All were fairly close in value except for 0.5 m, with a peak concentration of 18.5 μM. Peak concentrations for 16 m and 32 m were reduced and occurred at 30 min and 45 min, respectively. Second, smaller peaks formed or began to form later in the time course at 8 m, 16 m and 32 m. At dam 2, the initial concentration reached in the pool was 9.76 μM (Figure 12). The peak concentrations for 0.5 m and 2 m occurred at 15 min. Peak concentrations for 4 m, 8 m and 16 m occurred at 30 min. Peaks were reduced with each station. Peaks at 8 m and 16 m were rather flat. A second, smaller peak formed at 60 minutes in the pond.

Chloride concentrations show generally the same patterns in timing as the nitrate peaks. The chloride peak at 0.5 m is higher than that of the pool at dam 4 (Figure 13). Chloride peaked at 30 min and 45 min at 8 m and 16 m, respectively, but began to increase again later in the time series. At dam 2, the chloride peaks at 2 m and 4 m are higher than those of the pond and 0.5 m (Figure 14).

At dam 4, ratios of nitrate to chloride decreased early in the time course and began to increase later in the time course (Figure 15). Between 0.5 m and 4 m, approximately 4.3 mmoles or 61 g of nitrogen was removed at dam 4. The highest ratios occurred in the pond and at 0.5 m, at 45 min. The lowest ratios were at 2 m and 4 m at 30 min. At dam 2, ratios tended to decrease or remain steady until peaking later in the time course. Ratios in the pond increased steadily until peaking at 60 min (Figure 16).

The ratios of nitrate to chloride at the time of each station's peak nitrate concentration show similar patterns around the dams at dams 2 and 4, but different patterns at the stations farther downstream (Figure 17). At dam 4, the nitrate to chloride ratio remained fairly constant between the pond and 0.5 m. Between 0.5 m and 2 m, the ratio dropped considerably. The ratio increased slightly between 2 and 4 meters, then remained fairly constant throughout the rest of the reach (Figure 17). At dam 2, the ratio increased slightly between the pond and 0.5 m, then dropped
between 0.5 m and 2 m. The ratio increased considerably between 8 m and 16 m (Figure 17). The constant ratio between the pond and 0.5 m at dam 2 suggests that the passage of the pulse through the dam did not cause any nitrate uptake. Similarly, the ratio at dam 4 only rose slightly, indicating a minor amount of nitrate uptake. The substantial decrease seen in both dams between 0.5 m and 2 m indicates that nitrate uptake occurred in this section of the reach. At dam 4, the slight increase between 2 m and 4 m signifies a decrease in nitrate uptake. The amount of uptake remained constant at dam 4 throughout the remainder of the time series. At dam 2, the constant low ratio between 2 m and 8 m suggests that nitrate uptake persisted. The increase in the ratio after 8 m suggests that nitrate is either being generated by in-stream processes, or the stream is receiving an input of spring water with a high concentration of nitrate.

The distinct peaks of conductivity, nitrate and chloride at both of the dams affirm that the nutrient additions traveled through the dams as pulses, even though mixing the additive into the pond brought the pond to equilibrium nitrate and chloride concentrations. Cart Creek received rain the day before I performed the additions, so flow rates were high enough that day to push the pond water containing the additive through the dam as a pulse. The transit time of the pulses ended up being much shorter than initially anticipated. The steep increase in conductivity from the time point just prior to the conductivity peak and the peak at both dams shows sodium breakthrough; the drop in conductivity after the peak point illustrates the downstream movement of the pulse. Since chloride is a conservative tracer, reductions in the concentrations at the chloride peaks with successive downstream stations represents the dilution of the pulse as it moves downstream. Dilution was not seen in dam 2 until 8 m, where groundwater inputs may have been coming in. The chloride dilutions seen at dam 4 were typically smaller and more gradual than those seen at dam 2, so perhaps groundwater inputs were less of a factor at dam 4 (Figure 13, Figure 14).

The initial nitrate concentrations in the pond at both dams were lower than the concentration I aimed to reach by mixing in the additive (Figure 11, Figure 12). This may be due to the rise in water level that occurred after I surveyed the pond. I
tried to estimate how the boundary of the 100-L$^3$ section of pond may have shifted with higher water levels, but likely ended up mixing the additive into a larger area than I calculated for. The fact that the peak at 0.5 m in dam 4 is higher than the peak in the pond suggests that the additive was not necessarily mixed uniformly throughout the pond, and that a patch of especially high concentration was sampled at 0.5 m (Figure 11). In repeating this experiment, I would adopt a more effective mixing technique, perhaps by using a pump.

**Discussion**

Sediment characteristics did not necessarily reflect the heterogeneity that I expected to see among the different portions of the spatial mosaic created by the dam. The percentage of nitrate removed by the pond sediments was lower than predicted, given the expectation that ponds act as nitrate sinks. This corresponds with research that attributes the nitrogen sequestration in ponds to increased nitrogen residence times (Naiman & Melillo, 1984). Though the microbial communities in the ponds appear to be less effective at removing nitrate, the increased contact time of water and sediment allows for substantial reductions to occur in ponds.

The low rate of ammonium mineralization in the pond is surprising given that ponds are shown to be sources of ammonium (Margolis *et al*., 2001). Ammonium production in ponds is attributed to anoxic conditions, in which there is not enough oxygen for accumulated ammonium to be oxidized to nitrate. All of the sediments in this experiment were incubated under the same anaerobic conditions, thus removing the variability in hypoxia that occurs in a natural stream. Given that the percentages of organic matter in all of the sediments were similar, it is possible that ammonium in these sediments is affected more by dissimilatory nitrogen reduction to ammonia, in which nitrate is converted directly to ammonia, than by mineralization of organic matter.

The relative homogeneity of sediments in terms of C:N ratio and percent organic matter throughout the reach is surprising. I expected that the pond and dam would be composed of sandy, muddy sediment with significantly higher organic
matter content than the rocky downstream portions of the reach, but found that the entire reach was of a homogenous muddy consistency. I expected that the sediments in the dam and at 0.5 m downstream would have noticeably higher C:N ratios due to containing more wood. However, the C:N ratios throughout the reach are most similar to submerged vascular vegetation (personal communications, SES, 2015). This suggests that decomposing wood does not greatly affect the sediment composition in and below the dam, perhaps because the wood has not been decomposing for a long enough period of time. Future sediment sampling at this dam may yield higher C:N ratios as the wood continues to decompose.

The similarities among stream channel sediments and impoundment sediments may be due to the density of dams along this section of Cart Creek. The average density of beaver dams on a creek in northern Minnesota was reported to be 2.5 dams/km (Naiman et al., 1988). Dams 1-4 occurred within 0.5 km on Cart Creek, displaying a higher than average density that is causing the transformation of free-flowing sections of stream channel into impoundments. This may explain the overall lack of marked reductions in nitrate concentrations from above to below dams. Additionally, the overall low nitrate concentrations in Cart Creek ensure that any differences within a dam site or along the downstream transect are slight. These low nitrate concentrations in Cart Creek are consistent with expectations of a first-order stream in a temperate eastern forest in the fall. Margolis et al. found concentrations of less than 5 μM in a first-order stream on the Appalachian Plateau during all seasons of the year (2001). The data from Margolis show that the greatest nitrate reductions below dams occurred in a second-order stream, where background concentrations were up to six times higher than those of Cart Creek. The greatest reductions in Margolis’ study occurred in the summer, and the smallest reductions occurred in fall. Repeating this experiment at Cart Creek in spring and summer may yield different results.

The lack of nitrate uptake seen as the pulses passed through the dams indicates that the dams were not acting as trickle filters. As evidenced by the relatively quick transit of the pulses from the ponds to the 0.5 m stations, water moves through the dams fairly quickly. Although the denitrification potential of
sediment in dam 2 was relatively high, the contact time between water and the dam sediments is too short for denitrification to occur. The nitrate uptake that occurred between 0.5 m and 2m at both dams may be influenced by water traveling down a vertical gradient created by the hydraulic head. As water flows through the dam, it is thrust downwards into the hyporheic zone, where increased contact with sediments may promote nutrient uptake by microbial communities in the sediment. The regeneration of nitrate seen at 16 m at dam 2 may explain the high rate of nitrate removal seen in the sediment from 20 m during the incubation. If this section of the reach is receiving high nitrate inputs, the microbial communities in the sediment may be primed to quickly process large amounts of nitrate.

**Conclusions**

The nitrate uptake trends seen in Cart Creek illustrate variability of nutrient processing within relatively short reaches of stream. Variations may be explained by the interactions of biological and hydrological processes in Cart Creek. Several areas within the studied reach seem to harbor microbial communities with high nitrate processing potential, but high nitrate uptake was only seen where hydrological conditions promoted the contact of water with these sediment communities. The two abandoned dams I studied did not appear to be acting as trickle filters. However, the physical alterations to the stream channels caused by the dams likely influences the variability of nutrient processing within the stream reaches. The potential for denitrification within dams is high, so in streams with different hydrological conditions that promote more contact with dam sediments, it is possible that dams may incur more of a trickle filter effect. Nutrient pulse experiments should be repeated at Cart Creek in spring and summer when flow regime is different and changes in nutrient concentration along a downstream transect may be more pronounced. Additionally, the nutrient concentration comparisons along a downstream transect should be made continuously throughout coming years, as the beaver colonization status of Cart Creek evolves. The high density of dams, the presence of multiple abandoned dams, and the pond-like character of sediments and flow regime in channel stretches suggest that the section
of the creek studied here is reaching its maximum capacity for colonization. Downstream portions of Cart Creek, closer to rock dam 6, should be monitored for new beaver activity in the coming years. Habitat heterogeneity may be more pronounced in less densely colonized stream reaches, and nitrate reduction may be more pronounced in these areas as well.

The ecosystem alterations caused by the engineering activities of beavers are associated with the ecosystem service of nutrient reduction. Though the abandoned dams in this experiment did not show trickle filter effects, the hydrological and biological conditions that foster nutrient uptake are influenced by the presence of dams. Continued management plans for beaver will be important in eastern Massachusetts, where reduction of nutrient loading into estuaries is a valuable component of preventing eutrophication.

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**Literature Cited**

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Tables

**Table 1: Descriptions of six dams on Cart Creek.** Distance indicates approximate distance downstream from dam 1. Pond depths represent an estimate of the deepest point.

<table>
<thead>
<tr>
<th>Dam</th>
<th>Distance</th>
<th>Dam type</th>
<th>Description</th>
<th>Impoundment area estimate</th>
<th>Hydraulic head</th>
<th>Pond depth</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0 m</td>
<td>Breached beaver dam</td>
<td>Road built through dam Trickle filter with majority of flow moving through river right macro-pore</td>
<td>2500 m²</td>
<td>Not measureable</td>
<td>--</td>
</tr>
<tr>
<td>2</td>
<td>70 m</td>
<td>Abandoned beaver dam</td>
<td></td>
<td>60 m²</td>
<td>11 cm</td>
<td>25 cm</td>
</tr>
<tr>
<td>3</td>
<td>370 m</td>
<td>Active beaver dam</td>
<td>Dam built up behind a human-built stone stream crossing</td>
<td>1500 m²</td>
<td>80 cm</td>
<td>--</td>
</tr>
<tr>
<td>4</td>
<td>420 m</td>
<td>Abandoned beaver dam</td>
<td>Trickle filter with water moving through relatively uniformly</td>
<td>30 m²</td>
<td>20 cm</td>
<td>45 cm</td>
</tr>
<tr>
<td>5</td>
<td>570 m</td>
<td>Rock dam</td>
<td>Series of small rock clusters</td>
<td>Not present</td>
<td>Not present</td>
<td>--</td>
</tr>
<tr>
<td>6</td>
<td>920 m</td>
<td>Rock dam</td>
<td>Trickle filter</td>
<td>--</td>
<td>&gt;80 cm</td>
<td>--</td>
</tr>
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Table 2: Carbon to nitrogen ratios and percent organic matter (carbon + nitrogen) in sediments.

<table>
<thead>
<tr>
<th></th>
<th>C:N</th>
<th>% C+N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pond</td>
<td>16</td>
<td>16</td>
</tr>
<tr>
<td>Dam</td>
<td>25</td>
<td>11</td>
</tr>
<tr>
<td>0.5 m</td>
<td>19</td>
<td>20</td>
</tr>
<tr>
<td>6 m</td>
<td>25</td>
<td>14</td>
</tr>
<tr>
<td>20 m</td>
<td>19</td>
<td>25</td>
</tr>
</tbody>
</table>
Table 3: Changes in nitrate concentrations from above dam to below dam. All values expressed in terms of percent. Negative percentages indicate higher nitrate concentrations below dam.

<table>
<thead>
<tr>
<th>Dam</th>
<th>Percent nitrate removed</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>-42</td>
</tr>
<tr>
<td>2</td>
<td>14</td>
</tr>
<tr>
<td>3</td>
<td>-160</td>
</tr>
<tr>
<td>4</td>
<td>34</td>
</tr>
<tr>
<td>5</td>
<td>-10</td>
</tr>
<tr>
<td>6</td>
<td>24</td>
</tr>
</tbody>
</table>
Figures

Figure 1: Abandoned dams at Cart Creek. a) Dam 2 is characterized by a macropore opening on the river right side of the dam, where most of the flow trickles through. b) Dam 4 is characterized by uniform trickle flow through the dam.
Figure 2: Nitrate concentrations along a downstream transect in Cart Creek. Above dam samples taken within 0.5 m from top of dam. Below dam samples taken within 0.5 m from bottom of dam.
Figure 3: Phosphate concentrations along a downstream transect in Cart Creek. Above dam samples taken within 0.5 m from top of dam. Below dam samples taken within 0.5 m of bottom of dam.
Figure 4: Changes in nitrate concentrations over time in first sediment replicates.
Figure 5: Changes in nitrate concentration over time in second sediment replicates.
Figure 6: Percent of initial nitrate concentration removed by end of sediment incubation. Initial nitrate concentrations based on time 0 samples. Final nitrate concentrations based on time 4 (95 hour) samples. Error bars based on SEM.
Figure 7: Nitrate removal rates in incubated sediments. Removal rates calculated from difference between final and initial concentrations, averaged over 95 hours. Initial nitrate concentrations based on time 0 samples. Final nitrate concentrations based on time 4 (95 hour) samples. Error bars based on SEM.
Figure 8: Ammonium mineralization rates in incubated sediments.
Mineralization rates based on differences between ammonium concentrations at time 4 (95 hours) and time 0, averaged over 95 hours. Error bars represent SEM.
Figure 9: Conductivity readings during nutrient addition at dam 4.
Figure 10: Conductivity readings during nutrient addition at dam 2.
Figure 11: Nitrate concentrations over time course during nutrient addition at dam 4.
Figure 12: Nitrate concentrations over time course during nutrient addition at dam 2.
Figure 13: Chloride concentrations over time course during nutrient addition at dam 4.
Figure 14: Chloride concentrations over time course during nutrient addition at dam 2.
Figure 15: Nitrate to chloride ratios over time during nutrient addition at dam 4.
Figure 16: Nitrate to chloride ratios over time course during nutrient addition at dam 2.
Figure 17: Nitrate to chloride ratios at nitrate peaks. Vertical axis reflects spatial location of dam.
Figure 18: Nitrate to chloride ratios at nitrate peaks. 32 m point from dam 4 removed for detailed comparison of first 16 m between dams. Vertical axis reflects spatial location of dam.