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The Impact of Dams on Nitrogen Cycling in the Messalonskee Stream

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ABSTRACT

The Messalonskee Stream in central Maine has five hydroelectric dams on 16.6km. Each dam drastically changes the flow regime of the stream, dividing it into segments with different patterns of sediment settling and organic matter retention. I investigated how these disruptions impact nitrogen cycling, specifically nitrification rates above and below each dam. I expected higher nitrification rates above the dams, where levels of organic matter are higher, and lower rates below the dam where scouring removes organic matter and fine sediment from the streambed. I measured sediment nitrification rates with a nitrapyrin-inhibition assay and potential drivers of nitrification including sediment organic matter and pore water ammonia (NH_4^+) above and below each dam. Nitrification rates ranged from 0-1490 µg NH_4^+ g AFDM $^{-1}$ day^{-1} with an average of 105µg NH_4^+ g AFDM $^{-1}$ day^{-1} showing a wide range of variation with no consistent pattern between above and below sites. Variation among the five dam sites is due different distributions of sediment above and below the dams due to widely varying flow velocity.

ACKNOWLEDGEMENTS

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INTRODUCTION

1.1 The Impact of Dams on Streams

Dams present one of today's more complex environmental challenges. They are celebrated as landmarks of industry and used for low-carbon energy production, and yet dams are significant disruptions to riverine ecosystems that can cause long-term degradation of aquatic ecosystems. The U.S. Army Corps of Engineers has catalogued over 75,000 dams larger than five feet tall on rivers and streams across the country. These dams are created to generate hydropower, store water, control floods, or irrigate fields. However, dams also can damage ecosystems, harm economically-important fisheries, and impact recreational opportunities (Bednarek 2001). Many U.S. dams are legacies of the first half of the 20th century, and are structurally deteriorating with age. Dam failures can have serious environmental consequences as well as occasionally losses of property or human lives (Cenderelli 2000). To avoid this, deteriorating impoundments must be repaired, replaced or removed. Since the 1980s, more than 500 dams have been removed from rivers nationwide. In many cases, the cost of repair is so high, that removal is economically the best choice (Stanley and Doyle 2003). Additionally, the original purpose for which many older dams were constructed has changed by current economic conditions (Shuman 1995). By the year 2020, 85% of all dams in the United States will have surpassed their functional lifespan of 60-120 years (FEMA 1999).

Dams and dam removal is a contentious issue in Maine beginning with the removal of the Edwards Dam on the Kennebec River in 1999 (Bednarek 2001). Maine is at the forefront of dam removal, as the Edwards Dam was the first time the Federal Energy Regulatory Commission (FERC) ordered a dam to be removed for solely ecological reasons. On the Penobscot River, two dam removals—the Great Works Dam and the Veazie Dam—and a fish bypass at the Howland Dam have been planned as part of a basin-wide strategic plan to increase environmental health and yet maintain the same power-generating capacity (Opperman et al. 2011). For this project, as well as for the Edwards Dam, the most influential argument supporting dam removal has been to restore fish passage for native anadromous fish such as alewives, salmon, shad, and sturgeon (Shuman 1995, Day 2006). While this is a culturally and economically important goal,

dams impact many other ecosystem functions other than just fish passage, such as altering flow rates, changing phytoplankton and macrophyte communities, creating thermally stratified systems, increasing sediment deposition and nutrient retention above the dams, and leading to sediment and nutrient depletion below (Bednarek 2001).

Spatial and temporal variations in frequency, magnitude, duration, and regularity of flows determine the physical environment of a river as well as the biotic community it supports (Poff et al. 1997). Dams alter these natural flow regimes by blocking the river, storing excess water, and releasing it at times of peak power consumption. In many cases, impounded rivers experience greater weekly, daily, and hourly fluctuations than undammed rivers because flow is regulated to correspond with variations in power demand or water consumption (Gillilan and Brown 1997). For example, the Ocoee River in south eastern United States, regulated by the Tennessee Valley Authority, alternates between surging white-water and low-flow as water is diverted to power-producing facilities (Devine 1995). These extreme changes can cause physical scouring of the riverbed and can leave the stream devoid of fauna due to high boundary shear stress (Lignon et al. 1995, Camargo and Voelz 1998). Additionally, organisms are not adapted to such extreme daily variation since there is no naturally occurring analogue, creating a very stressful environment. Some effects of high flows from hydroelectric dams are increasing drift of macroinvertebrates (Bunn and Arthingon 2002) and stranding fish in low water areas (Poff et al.1997).

By blocking normal river flow, dams raise water levels, creating reservoirs with lake-like habitat characteristics and often resulting in changes in species composition of fish and macrophytes from lotic to lentic species. Reservoirs also often result in warmer epilimnetic water and cooler hypolimnetic water than an unregulated river. These thermal layers rarely mix, creating a permanently stratified system (Bednarek 2001). Many dams have water intakes at the bottom of the reservoir causing a release of cold hypolimnetic water downstream. The thermal shock from this sudden flush of cold water can result in fish kills downstream (Ryan 1991).

Another consequence of decreased flow above the dam is sediment settling and long-term deposition (Bednarek 2001). Powers et al. (2013) found that small impoundments are sites of long term nutrient and sediment storage in North America,

creating hybrid wetland-like ecosystems that grow over time. Sediment accumulation due to dams also increases nutrient retention above the dam. In contrast, water devoid of its sediment load is released below the dam limiting the benthic nutrients available to downstream organisms. These “clear-water” releases have numerous effects such as increased erosion, bank collapses, and channel incision as the stream regains sediment and nutrient equilibrium by picking up fine sediment (Bednarek 2001). One very important aquatic nutrient that could have altered concentrations above and below dams is nitrogen (N).

1.2 The Nitrogen Cycle and Nitrification

In aquatic systems, N is both an important nutrient and a potential pollutant. Insufficient N will inhibit primary productivity—especially in N-limited systems—causing a decrease in productivity at all other trophic levels. But too much nitrogen can cause eutrophication and algal blooms than can be harmful to aquatic ecosystems and human health (Vitousek 1997). Elevated concentrations of nitrate (NO_3^-) in drinking water has been shown to lead to blue baby syndrome because of its inhibition of hemoglobin (Knobelach et al. 2000). Humans have doubled the rate of N inputs to terrestrial systems, mostly due to fertilizers, and this has significantly increased nitrogen loading to aquatic and marine environments (Vitousek 1997). The most drastic instance of nitrogen loading in the United States is seen in the Mississippi River delta when high-nutrient runoff from the agricultural watershed flows collects in the river and causes massive algal blooms in the Gulf of Mexico. The resulting die-off causes a hypoxia zone that changes in size every year based on runoff from the Mississippi River. In 2002 it covered an area of 20,700km^2 (Rablais et al. 2002). However, impacts of excess N loads have been seen in watersheds of all sizes (Vitousek 1997). There are even anthropogenic N subsides to lakes far removed from human development due to atmospheric deposition, showing that disturbances to the nitrogen cycle are truly a global phenomenon (Holtgrieve et al. 2011).

Nitrogen exists in many forms in the environment, and is transformed by a variety of organisms by both assimilatory and dissimilatory processes (Figure 1).

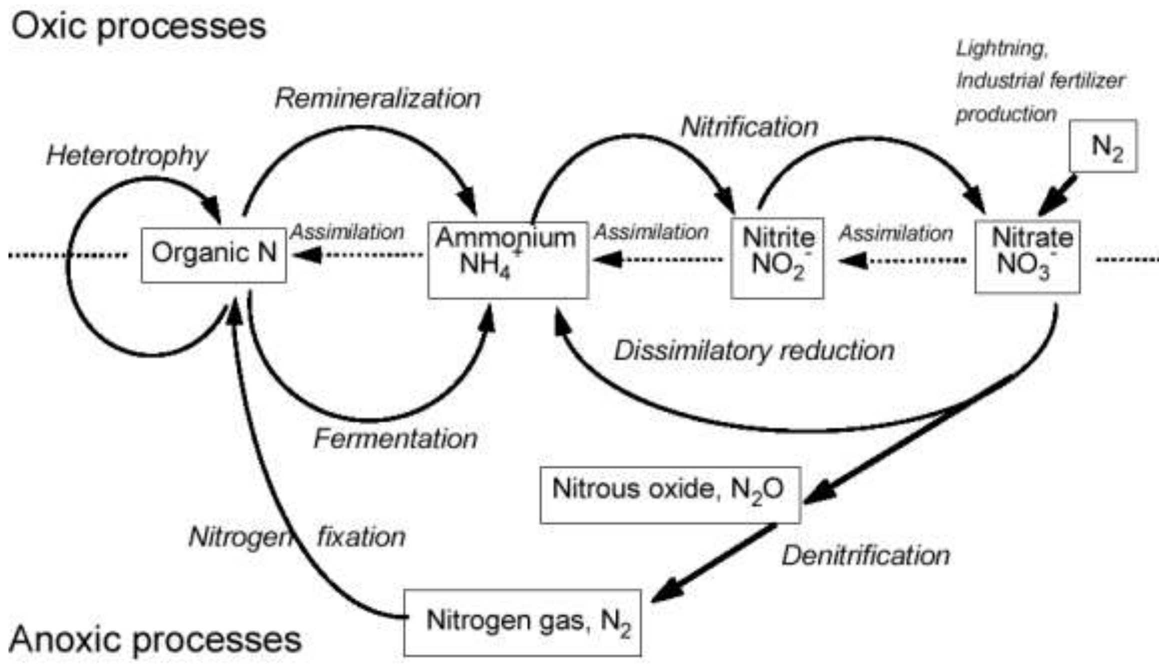


Figure 1**.** The aquatic nitrogen cycle (Dodds and Whiles 2010).

Nitrification is a two-step process by which ammonia (NH_4^+) is oxidized to nitrite (NO_2^-) by *Nitrosomas* and then further oxidized by *Nitrobacter* into nitrate (NO_3^-). These bacteria are chemolithoautotrophs that live in the top three centimeters of the benthic sediment, and use the oxidation of ammonia as their energy source. It is a dissimilatory process because the nitrogen is transformed without being consumed by the organism (Dodds and Whiles 2010). Nitrification is important because it is a vital link in the N cycle that results in several forms of N available at any one time. Additionally nitrification is often coupled with denitrification, an important energy-yielding process as well as a way to remove nitrogen from the ecosystem (Fenshel et al. 2000). A series of 15-N tracer studies of headwater streams as part of the LINX (Lotic Intersite Nitrogen eXperiment) found that nitrification rates were responsible for 50% of the variation in stream NO_3^- rates, signifying the importance of nitrification to whole-stream nitrogen cycling (Peterson et al. 2001) However this study was conducted primarily in small

streams with low background nutrient concentrations. In larger rivers, it is likely that most of the variability in NO_3^- concentrations is from terrestrial nitrogen loading, and the contribution of nitrification is small in comparison (Strauss et al. 2004).

Most primary producers prefer NH_4^+over NO_3^- for biological assimilation because they do not need to reduce it before use, as they do with NO_3^- (Grimm and Fisher 1986, Stanley and Hobbie 1981). However, NO_3^- is more often more available in aquatic systems because NH_4^+ can be adsorbed to sediment particles, and remain in one place for longer without being washed downstream (Berhardt et al. 2002). Nitrification is essential to make nitrogen more available in the ecosystem, even if it in the less preferred form.

The two main factors affecting nitrification rates are the availability NH_4^+ and the availability of oxygen in the sediment (Fenshel et al. 2000). However, these two factors can be affected by many variables. Sediment NH_4^+ depends on concentration in the water, the quality of the carbon (C) source available from decomposing organic material, and plant uptake. A high C:N ratio in the soil results in low production of NH_4^+, but also a significant amount of carbon that consumes oxygen. Oxygen is controlled by soil texture and water content, and respiration of microbes in the soil, as can be seen in Fig. 2 below (Fenshel et al. 2000).

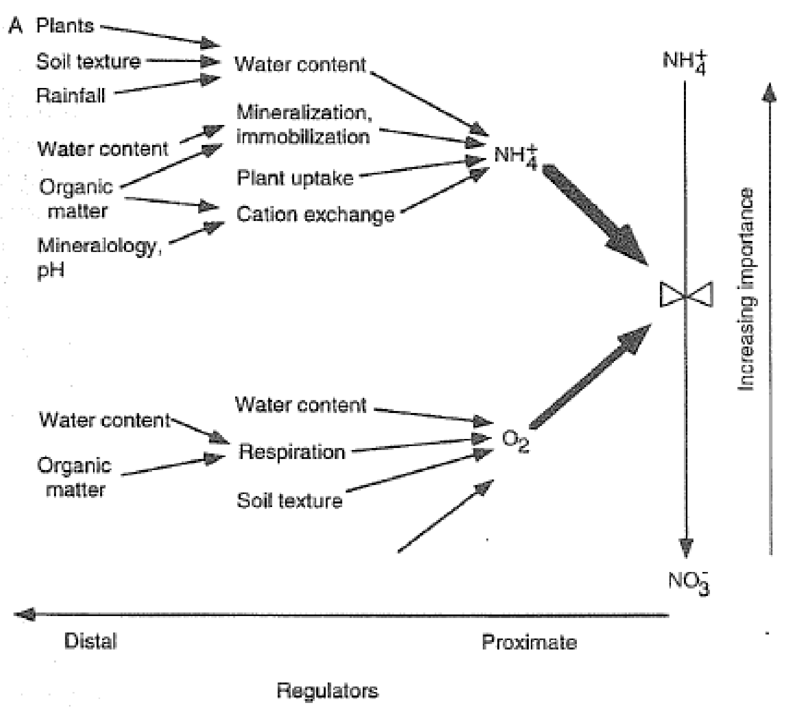


Figure 2. The various controls of nitrification in streams (Fenshel et al. 2000).

Nitrification is most efficient when oxygen penetration into the sediment is high enough to support this aerobic process (Fenshel et al. 2000). NH_4^+ is bound up in the soil and pore-water spaces, but nitrification cannot happen without oxygen in the sediment as well. Oxygen penetration is increased by bioturbation from burrowing macroinvertebrates (Pelegri et al. 1996), and possibly by plant roots (Fenshel et al. 2000). Additionally, nitrification rates can decrease as quality of DOC increases. In sediments with a high percent organic matter, there is larger percentage of heterotrophic bacteria that require ammonia for assimilation. These bacteria can outcompete the nitrifying bacteria for ammonia, decreasing the amount of ammonia available for nitrification (Strauss and Lamberti 2002). However, it has been documented that in terrestrial studies, nitrification also can be inhibited when the quality of organic matter is very low and included a significant proportion of other plant-derived compounds such as polyphenols and tannins (Baldwin 1983). There is a critical C:N ratio of ~20. Below this (C:N < 20) nitrification rates are regulated by NH_4^+ availability, while at C:N >20 nitrification rates are controlled by the quantity and quality of organic carbon (Strauss et al. 2002). pH can also be a controlling factor; nitrification is inhibited at low pH but enhanced at near-neutral pH (Strauss et al. 2002).

1.3 The Impacts of Dams on Controls of Nitrification

Dams have extensive impacts on stream structure and nutrient retention, making it likely that they will impact nitrification rates. Reservoirs increase settling of sediment above the dam. This accumulation of sediment is often high in organic matter, stimulating decomposition and production of NH_4^+. Higher ammonia would likely increase nitrification rates. Strauss (2004) found higher nitrification rates in impounded and backwater habitats of the upper Mississippi river compared to side channel and main channel habitats. This difference was attributed to higher concentrations of NH_4^+ in the sediment as well as total N. However, if there is too much decomposition in the sediment above the dam, it can create anoxic conditions in the sediment, inhibiting nitrification process. However, this is only a consideration in ecosystems with higher than natural inputs of organic matter.

Below the dam, the fast water flow erodes fine sediment out the streambed decreasing the amount of organic substrate available to nitrifying bacteria, as well as the pore-water spaces to needed to store ammonia stored in the sediment. Less available carbon inhibits the activity of decomposing bacteria, resulting in less ammonia production, further decreasing nitrification rates. Increased flow could create highly-oxygenated conditions, that would normally stimulate nitrification, but without the ammonia, this is not possible.

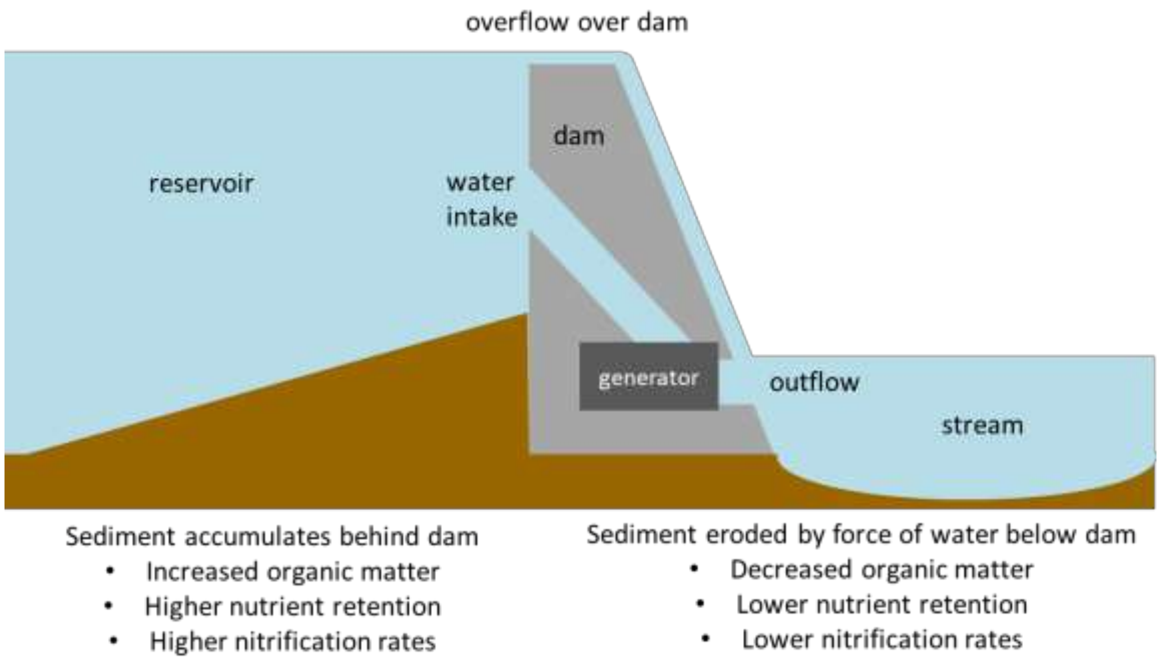


Figure 3. A conceptual model of how dams affect the controls of nitrification rates in a stream ecosystem.

1.4 The Impact of Wastewater Treatment Effluent on Nitrification Rates

Wastewater treatment plants can have a substantial impact on aquatic systems, altering nutrient regime and biological community (Wakelin 2008). Wastewater effluent has been shown to have drastically higher NH_4^+ concentrations at point of discharge. This ammonia subsidy increases nitrification rates and heterotrophy in the stream benthos in a geographic pattern with heterotrophic bacteria closer to the effluent source and nitrifying bacteria more dominant farther downstream (Cébron et al. 2003). In one study, effects were greatest 400m downstream where a decrease in flow increased sediment deposition

(Wakelin 2008). However, Cronk (1996) found that wastewater effluent inhibited nitrification rates due to low oxygen availability.

1.5 The Messalonskee Stream

The Messalonskee Stream in central Maine is the only outflow of the Belgrade Lakes watershed: a glacially-formed chain of seven interconnected lakes with a catchment area of 458km^2 (Curtis 2006). The stream begins in the center of Oakland, Maine, traveling through open land and residential areas and then ends at the Kennebec River in the southern end of Waterville, Maine. Along this path—a total length of 16.6km—there is a wide variety of land uses and five dams affecting stream structure and inputs.

Thousands of years ago, the Belgrade Lakes drained directly south to the Kennebec River in Augusta, but when that outlet was blocked by glacial till, the force of the water carved out a new path to the northeast and then southwest to empty into the Kennebec in southern Waterville. This massive flow of water resulted in a series of steep waterfalls that prevented a significant alewife population from being established in the stream as in other Kennebec tributaries such as the Sebasticook (Watts, personal communication) although it is home to American eels (Barbin and McCleave 1997).

Throughout the history of Oakland and Waterville, the stream has been the site of numerous factories, dams, and dumping sites. The Messalonskee Stream's narrow and deep streambed facilitated damming for powering mills and factories. The first dam was built as early as 1778 (Marriner 1968). Industrial development in Central Maine led to bigger factories and dams on the stream such as the Dunn Edge Tool Company and the Cascade Woolen Mill, both in Oakland (Marriner 1975). Additionally, the stream's constant and powerful water flow led it to become the site of the first hydroelectric dam in Maine in 1901, built by the Messalonskee Electric Company (Plotcher 2007). Propelled by the economic success of providing electricity to the people of Waterville, this company grew to become Central Maine Power and installed four hydroelectric dams on the Messalonskee Stream that still remain today (Marriner 1977) although they have been sold to Essex Hydro LLC in Boston (Watts, personal communication).The stream was also used as the communal sewer for the homes and businesses along it,

because they were built so close to the stream that there was no room for a septic system. Dumping stopped in the 1980s when Waterville built a sewer system (Grenier, personal communication). The Oakland Wastewater treatment plant stopped dumping their treated water into the stream in 2012 (Hongoltz-Hetling 2012).

While dumping of sewage has stopped, five dams remain on the stream today, including one with a half-mile pipe diverting the majority of the flow towards the dam away from its original path. Having so many dams on the same stream creates unique laboratory for investigating the impacts of dams on benthic organic matter and nutrient cycling.

1.6 Research Questions and Introduction of Thesis

The focus of this project is to investigate how dams affect the distribution of the various nitrogen forms in the stream water and benthic sediment, as well as the rates and controlling factors of nitrification. Five dam sites on the Messalonskee Stream will be compared to a reference site on the same stream, but located as far from the dam sites as possible. Above- and below-dam sites will be compared to each other, as well as to the reference site, to see if the impacts on nitrification rates and controlling factors are more significant one side of the dams. I suspect that nitrification rates will be higher above dams where there is more available ammonia due to a collection of organic sediments stimulating the release ammonia. Downstream of the dams will have lower nitrification rates because the sediment-deprived water discharged from the dam will not have enough substrate to support large populations of nitrifying bacteria. Downstream effects could potentially be exaggerated at the dams towards the mouth of the stream due to cumulative effects of the five dams on the stream. Additionally, the effects of wastewater treatment effluent on nitrification rates will be investigated.

Research Questions:

1. Does the presence of dam impact stream nitrification rates?
2. Is this difference more apparent above or below the dam?
3. Do a series of dams on the same stream result in cumulative downstream effects?
4. Does historic wastewater effluent impact stream nitrification rates?

METHODS

2.1 Site Selection and Field Sampling

For each of the five dams on the Messalonskee stream, I chose a sampling site above and below the dam. The Messalonskee Stream is at least 30 feet deep in some places, and mostly bedrock, so finding a spot with safely accessible sediment was sometimes a challenge. For most of the dams, I was able to find an access point just above and below the impoundment, though sometimes I had to move slightly farther downstream due to dangerously high flows. The distances from the dams ranged from 5 to 500m away from the dams. The only outlier is the Rice Rips Hydroelectric Station (Dam 3) where the water is diverted in a half-mile pipe before the stations, so I sampled at the start of the pipe. Additionally, I took a sample near where the Oakland Wastewater Treatment recently stopped dumping its treated water into the stream. An additional site was a relatively un-impacted area of the stream with no dams or other human influence nearby used to compare to the various human-impacted sites. All field sampling and laboratory processing was completed in October 2013.

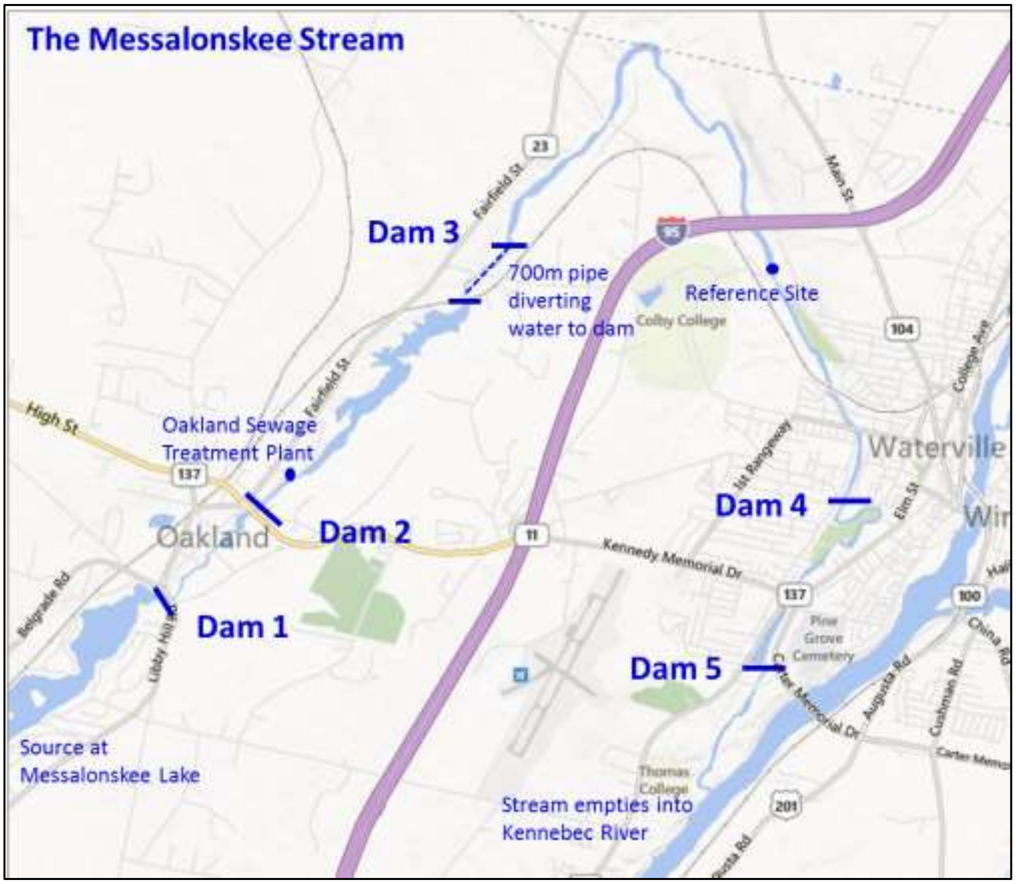


Figure 4. A map of the Messalonskee stream and all sampling locations (adapted from Bing maps).

2.2 Nitrification Assay by Nitrapyrin Inhibition

The same day as sampling, I set up the nitrification assay. I filled six flasks with slurries of 25mL sediment and 80ml unfiltered site water; three of these flasks received 10uL of 10% nitrapyrin in DMSO, and the other three received 10uL DMSO. I performed an initial extraction with potassium chloride. I shook the flask to suspend all settled sediment then syringed out 6mL to combine with 6mL of 2N potassium chloride in a15mL centrifuge tube. The tubes were shaken periodically for 40 minutes then centrifuged down the sediment at 5600 rpm for 8 minutes. After centrifuging, the supernatant was decanted and filtered into a glass scintillation vial. The remaining sediment slurry in the flasks was incubated on the shaker table at 175 rpm for three days and then extracted by the same process as described above. Nitrification was measured as the difference in the ammonia concentrations between day three of the paired inhibited and control flasks (Strauss et al. 2002; Arango et al. 2008; Bruesewitz et al. 2012). The

ammonia concentrations in the extractions were measured with a Lachat (Hach Instruments) using standard colorimetric methods.

2.3 Pore-Water Ammonia Extraction with Potassium Chloride

From each sample, I tared an empty 50mL centrifuge tube, added 12-25g of wet sediment and re-weighed the tube, then added a mass of 2N potassium chloride equal to the mass of sediment. I shook the tubes on the shaker table for 10 minutes to and then centrifuged down the sediment at 3000rpm for 12 minutes, and decanted and filtered the supernatant into a glass scintillation vial (USGS Technical Operating Procedure). This extraction removed the nutrients bound up in the sediment to make them available for analysis, giving a background level of ammonia and nitrate in the sediment.

2.4 Sediment Organic Matter

From each sediment sample, I took three replicate 5ml sub-samples and put these in pre-ashed weighing tins. These subsamples were dried in the drying oven, weighed, ashed in the ashing oven, and then re-weighed to determine the total amount of organic matter in the sediment. The equation to calculate percent ash free dry mass is:

$$\%AFDM = \frac{(Ashed\ sample\ mass\ -\ Dry\ sample\ mass)}{Dry\ sample\ mass\ - Weigh\ tin\ mass} \times 100$$

This calculation gives the organic matter content of the sediment which can be used to investigate if organic carbon is a controlling factor of the nitrification process

2.5 Water Chemistry

While sampling at each site, I also collected three 60mL bottles of filtered stream water to get background concentrations of ammonia and nitrate in the stream water. These water samples as well as the analytes from the nitrification assay and pore-water extractions were analyzed on a Lachat Quick-Chem 8500 Flow-Injection Analysis System. The methods used were nitrate/nitrite reduction by ultraviolet light with a detection limit of 50µg N/L (Method 10-107-04-6-A) and ammonia determination with the alkaline phenol method with a detection limit of 5µg NH_4^+/L (Method 10-107-06-1-Q).

2.6 Statistical Analyses

All statistical tests were performed in Stata 12.1 (StataCorp). Above dam, below dam, wastewater treatment plant, and reference sites were compared with a series of t-tests. The effects of the various controlling factors on nitrification rates were explored with a multiple linear regression. Distance from sampling site to dam, as well as cumulative geographic effects down the whole stream length were investigated with linear regressions.

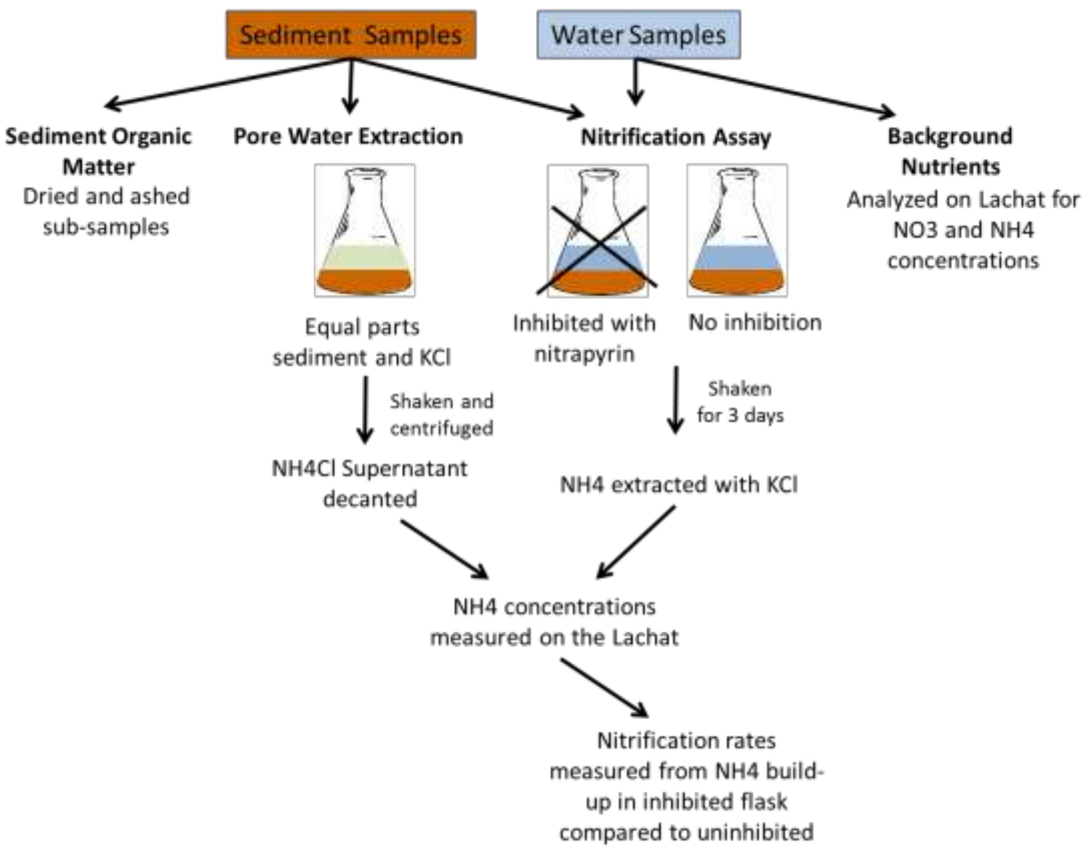


Figure 5. A diagram summarizing the various methods of this study.

RESULTS

3.1 Relationships among Controlling Factors

Despite wide variation among all samples, there was a general trend of higher percent organic matter in the benthic sediments associated with higher pore-water ammonia concentration (linear regression, $r^2 = 0.422$, $p < 0.001$) (Fig. 5). However, nitrification rates were not associated with any trend in organic matter, in-stream ammonia or pore-water ammonia (multiple linear regression, F = 0.44, $p = 0.7295$).

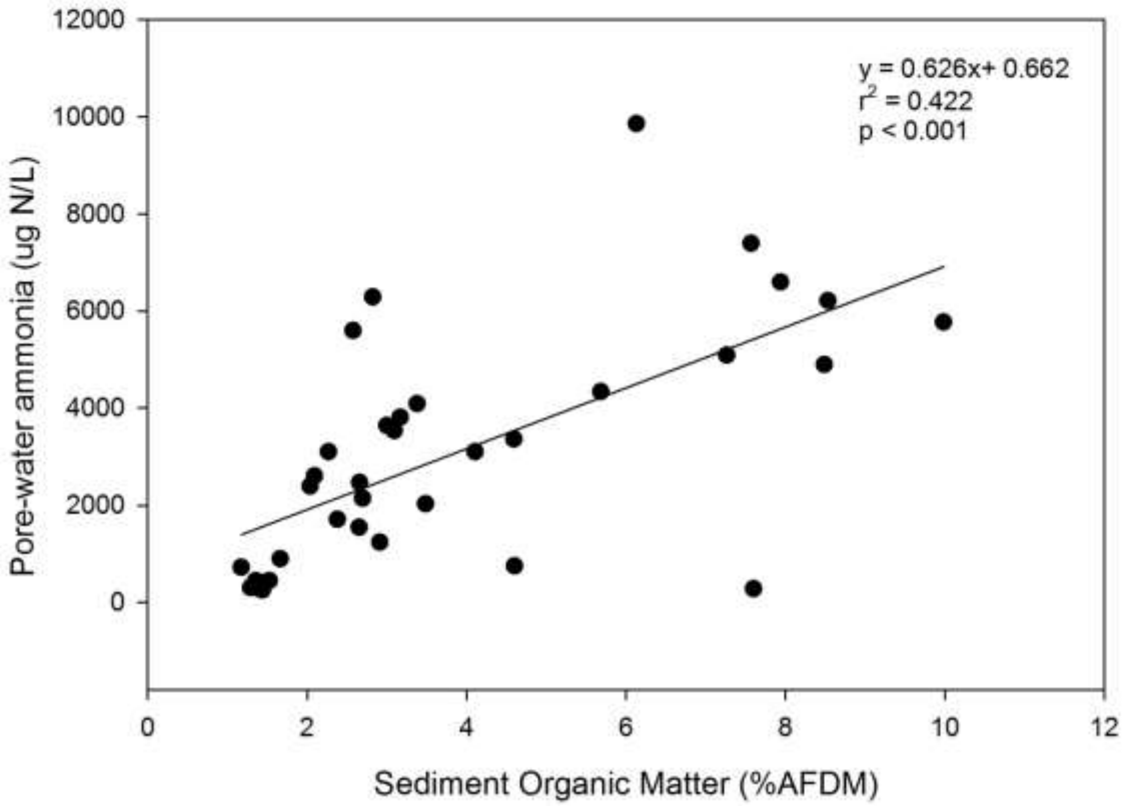


Figure 6. A linear regression of sediment organic matter and pore-water ammonia concentration.

3.2 Effects of Dams on Controls and Nitrification Rates

Organic matter was low and varied from 1-10% of total sediment among all sites. The combined dam sites were significantly lower in percent organic matter than the reference site ($n_1 = 27$ $n_2 = 3$, $t = -3.202$, $p = 0.0017$; Figure 7). The only exception is above dam 1 (site 1A) where Messalonskee Lake becomes Messalonskee Stream. 1A was much higher than all downstream dam sites suggesting that a large portion of the organic matter that would be carried downstream is instead retained in the lake and never makes it to the stream. The higher percent organic matter at the reference site is due to the fact that the water slows down enough for deposition of suspended dissolved organic matter onto the sediments.

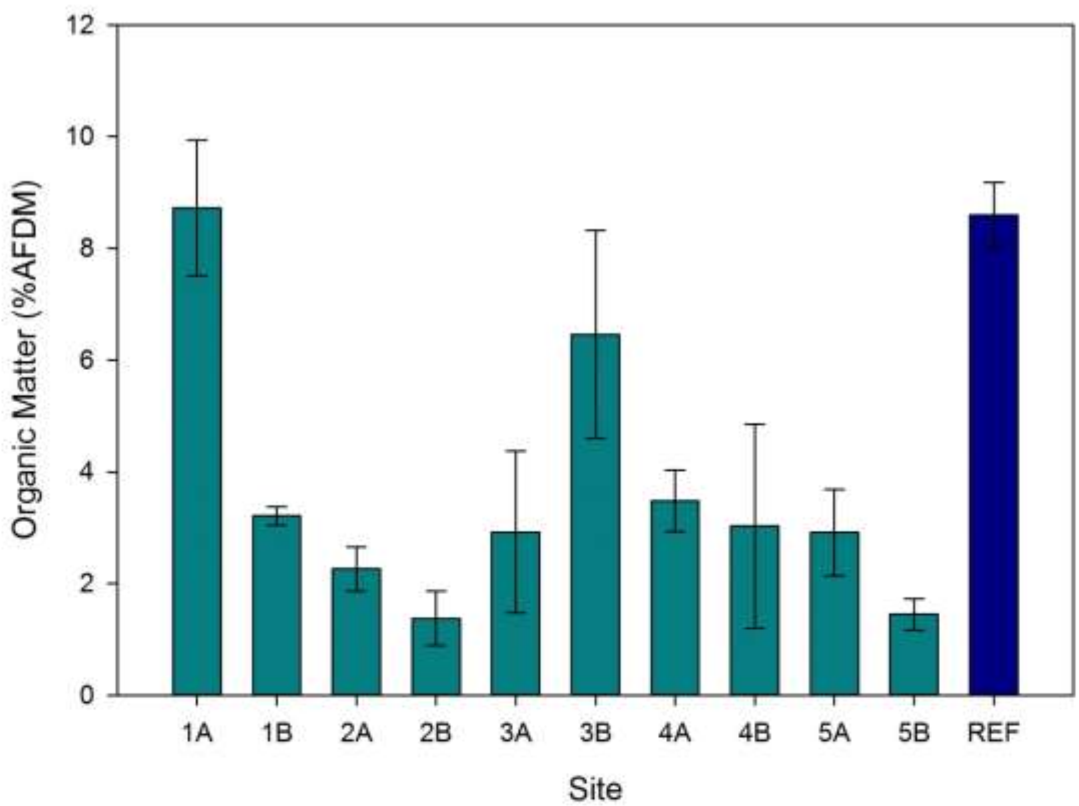


Figure 7. Organic matter content of the sediment, measured as percent ash-free dry mass, at all sites. Site numbers represent the number of the dam (1-5), and A or B designates an above or below dam site. All sites are arranged in order from upstream to downstream except for the reference site (REF). Values are the mean of three replicates per site; error bars represent one standard error.

Among all sampling sites, sediment-bound pore water ammonia varied from 257-9860 µgN/L. All dam sites had significantly lower pore water ammonia concentrations than the reference site, except for above Dam 1, and both sites at Dam 3, indicating that the dams are creating different environmental conditions than the free-flowing stream section ($n_1 = 27$ $n_2 = 3$, $t = -1.9342$, $p = 0.0316$; Figure. 8). Pore water ammonia concentrations at all sites were higher than surface water concentrations which ranged from 0-0.169mgN/L. This suggests that the ammonia already bound up in the sediment is retained, but not much more is produced in the stream, perhaps due to low levels of decomposition in the benthos.

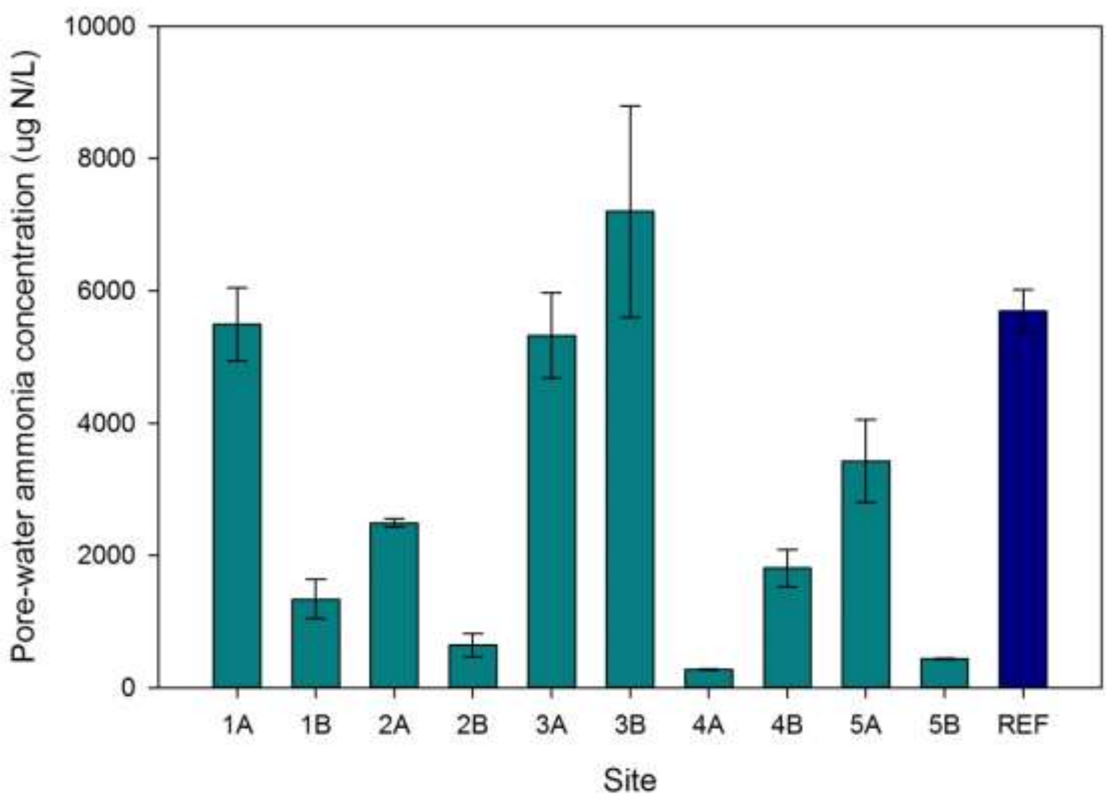


Figure. 8. Pore-water ammonia concentrations at all sampling sites, as measured by a potassium chloride extraction. Site numbers represent the number of the dam (1-5), and A or B designates an above or below dam site. All sites are arranged in order from upstream to downstream except for the reference site (REF). Values are the mean of three replicates per site; error bars represent one standard error.

Nitrification rates ranged from 0-1490 μg NH_4^+ g AFDM $^{-1}$ day^{-1} with an average of 105μg NH_4^+ g AFDM $^{-1}$ day^{-1}, showing a wide range of variation. Although the controlling factors were impacted by the presence of dams, the measured nitrification rates at each dam site were not significantly different from the reference site ($n_1 = 27$ $n_2 = 3$, $t = -1.0827$, $p = 0.1441$)

3.3 Effects of Wastewater Treatment Plant on Nitrification Rates

The sediment sampled near the Oakland Wastewater Treatment Plant was significantly lower in pore water ammonia ($n_1 = 2$ $n_2 = 3$, $t = 4.9686$, $p = 0.0078$) and sediment organic matter ($n_1 = 2$ $n_2 = 3$, $t = 5.6791$ $p = 0.0054$) than the reference site. The nitrification rate was not significantly different from the reference site ($n_1 = 2$ $n_2 = 3$, $t = 1.5274$, $p = 0.1121$)

3.4 Differences Among Above and Below Sites

Nitrification above Dam 1 was measured to be 227 ± 53μg NH_4^+ g AFDM $^{-1}$ day^{-1} while below the dam it was 11 ± 72μg NH_4^+ g AFDM $^{-1}$ day^{-1}. The same pattern was repeated at Dam 2 with a measured rate of 530 ± 197μg NH_4^+ g AFDM $^{-1}$ day^{-}above the dam and 19 ± 73μg NH_4^+ g AFDM $^{-1}$ day^{-}. However Dams 3 and 5 had the opposite effect of higher nitrification below the dam and below detection at the above dam sites. Dam 3 had nitrification rates 21 ± 35μg NH_4^+ g AFDM $^{-1}$ day^{-} above the dam and rates of 480 ± 508 μg NH_4^+ g AFDM $^{-1}$ day^{-1} below. The extremely high standard error demonstrates the heterogeneity of nitrification process and the wide level of variation even within one sediment sample since. Dam 4 had almost no substrate above or below to sample explaining comparable low nitrification rates of above the detection of the Lachat above the dam and 36 ± 54μg NH_4^+ g AFDM $^{-1}$ day^{-1} below the dam (Figure 9).

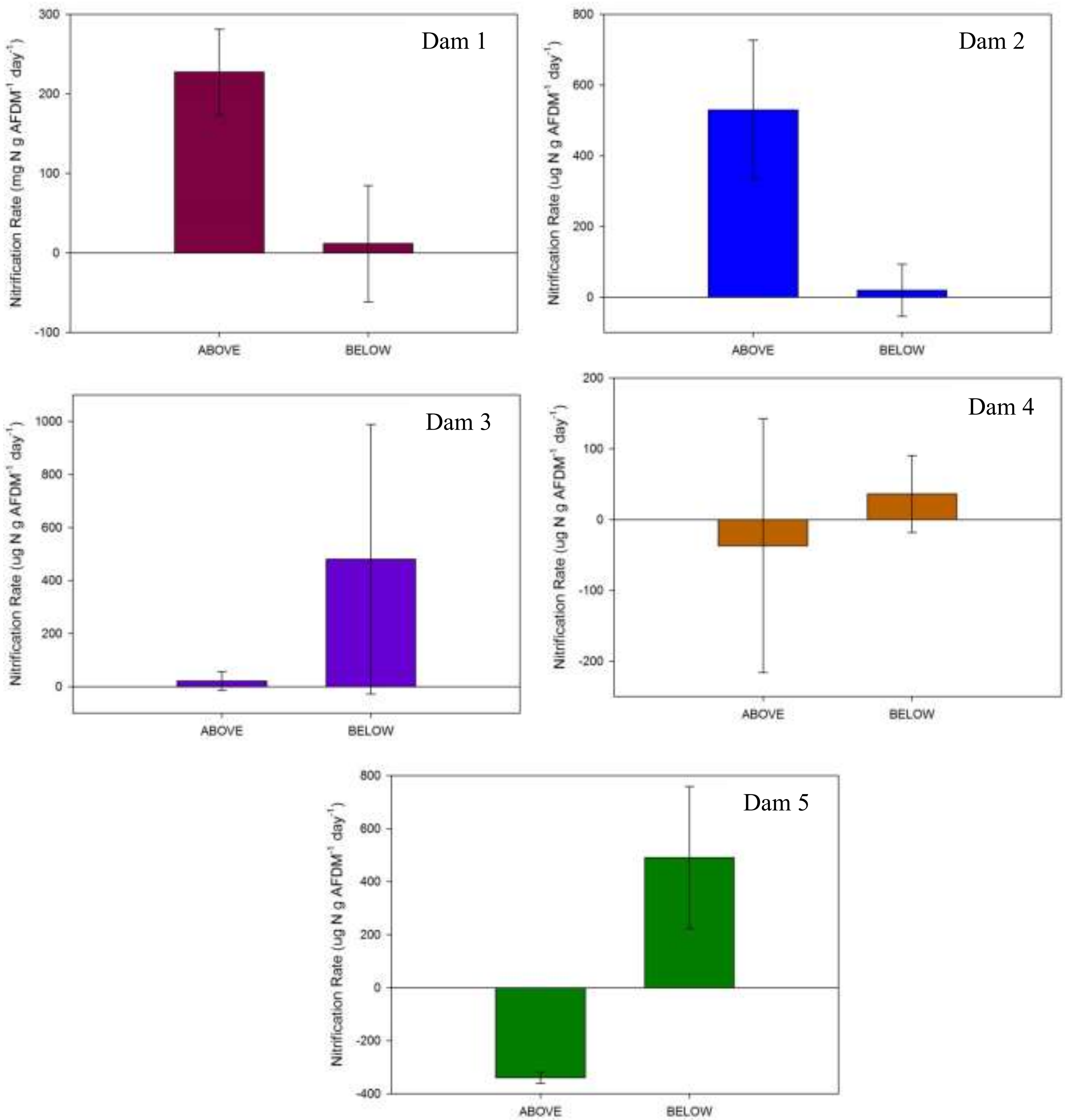


Figure 9. Nitrification rates above and below each dam. Values are the mean of three replicates; error bars represent one standard error. Note that the graphs have different scales on the y-axis to highlight above/below differences at each dam rather than comparison of rates across all five sites.

3.5 Landscape-level trends

Over the course of the stream from the Belgrade Lakes to the Kennebec River, pore-water ammonia concentrations vary, while stream water nitrogen concentrations and nitrification rates stay constant. The pore-water ammonia of the stream benthos follows a general trend of lower concentrations at either end of the stream where dams cause areas of fast flow and higher ammonia concentration in the middle where slower flows allow for sediment deposition and microbial processing (Figure 11). The lack of variation in stream water nitrogen concentrations suggests that while ammonia is getting deposited, it is not being processed. If nitrification were occurring, stream water nitrate concentrations would increase and ammonia concentrations would decrease, but both stay constant (Figure 12).

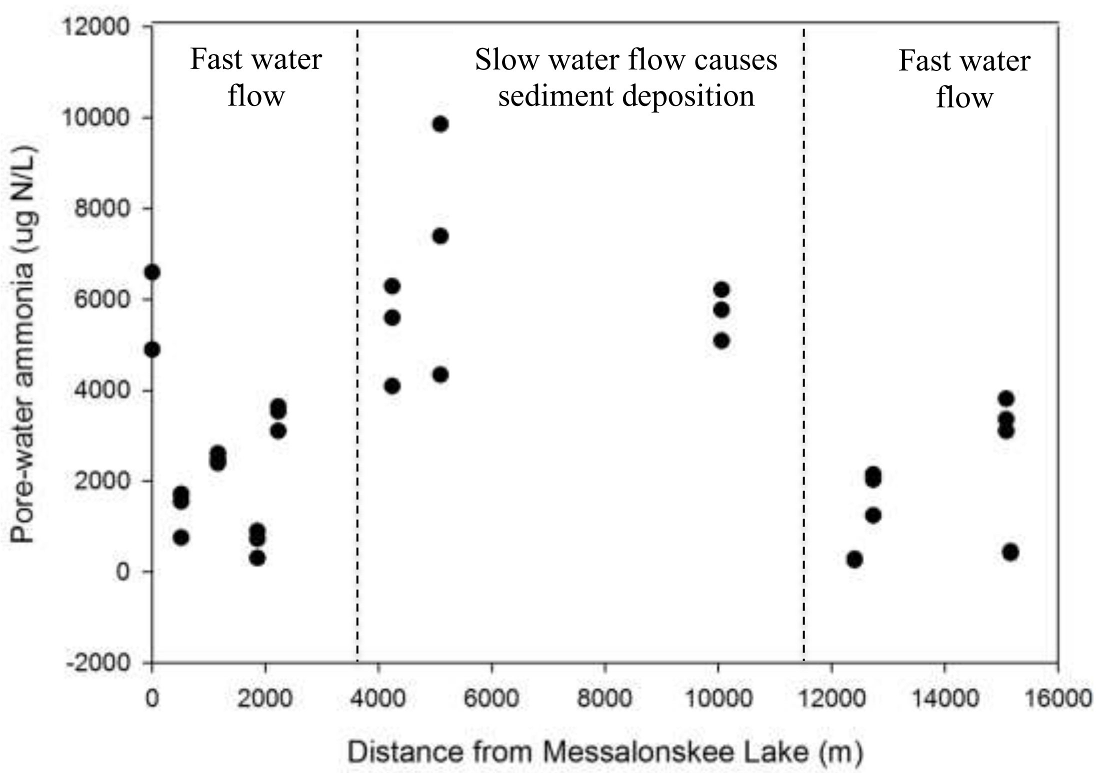
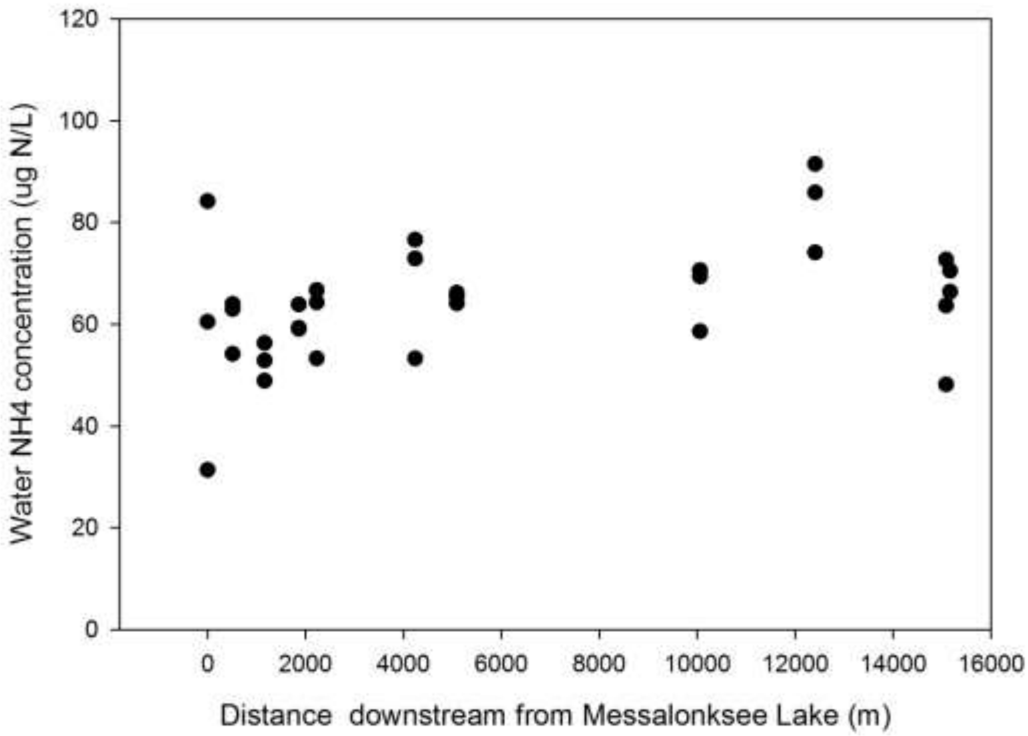


Figure 10**.** Geographic pattern of increasing and then decreasing concentration of pore water ammonia in the stream showing areas of sediment deposition due to slow flow.



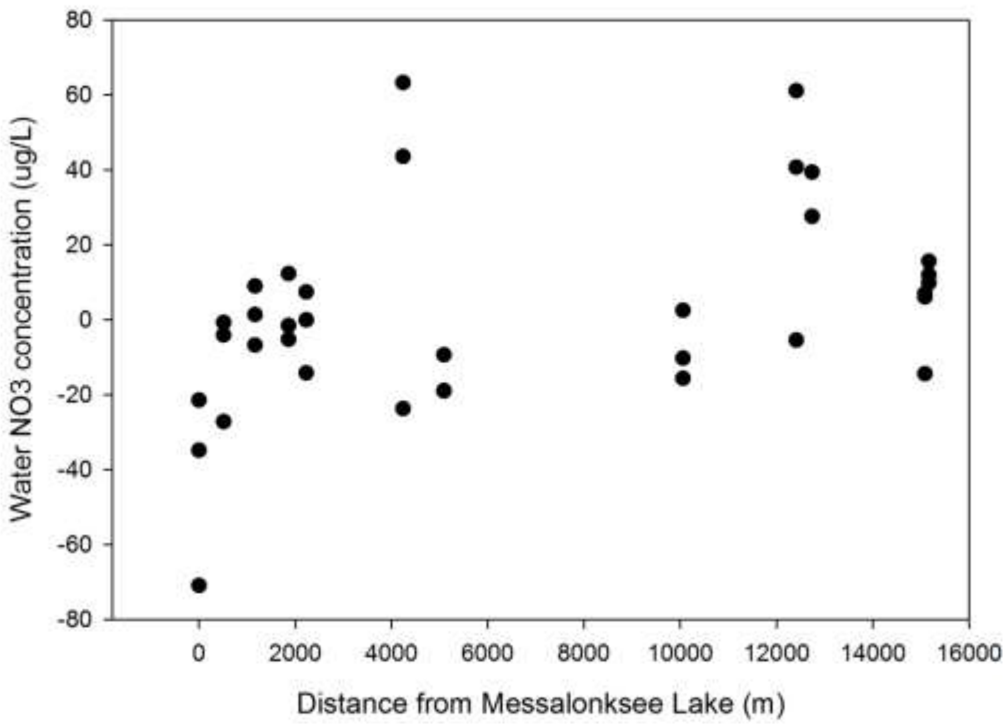


Figure 11. Constant ammonia concentration (above) and nitrate concentrations (below) throughout the whole length of the Messalonskee Stream.

DISCUSSION

4.1 Factors Contributing to Variation in Measured Nitrification Rates

There was wide variation in the nitrification rates at dam and reference sites. Some dam sites had higher nitrification rates than the reference site, and some had lower rates, without any consistent pattern among above- and below-dam sites. The first two dams followed the expected pattern of increased nitrification above the dam and decreased nitrification below, but this pattern was reversed in the other three dam sites. The fact that all five dams are on the same stream means that they are not independent replicates. Five dams in succession on a relatively short stream makes the above site of one dam also the below site of the dam upstream of it, complicating any above/below comparisons in nitrification rates.

Additionally, variation in measured nitrification rates across all samples is at least partially due to different sampling days, with different background water levels, as well as difficult sampling conditions. Although all sampling occurred in the same month with the same weather patterns, the discharge of the Messalonskee Stream is controlled by the hydroelectric dams meeting the power demand rather than environmental factors, and thus can vary significantly day to day. Stream flow has been called the “master variable” regulating all other factors of the ecological integrity of riverine systems (Poff et al.1997, Bunn and Arthington 2002) and it played a significant role in the variation in this study. Sampling below Dam 2 and Dam 3 was limited by unsafe conditions caused by fast turbulent flow off the dam, resulting in sampling spots that were not right below the dam, and not fully representative of below-dam conditions. Additionally, the substrate below Dams 3, 4, and 5 had been completely eroded out in the century that these dams have been in place, leaving only a bedrock channel. This made it hard to find sufficient substrate to sample.

4.2 Context of Similar Studies of Nitrification Rates

The nitrification rates measured in this investigation are in the range of other stream nitrification studies. Messalonskee Stream rates were higher than an average headwater stream (Strauss and Lamberti 2002) but lower than in agricultural streams or

lakes (Kemp and Dodds 2002, Bruesewitz et al. 2012). In a study of 19 sub-watersheds within the Hubbard Brook Experimental Forest, measured rates ranged 0-17,700 $\mu g\ N\ m^{-2}\ day^{-1}$ (Bernhardt et al. 2002). One key difference between the literature and this study is that other studies measured rates across several streams to come up with an average measure of nitrification rates, while the variation in rates of this study is all within the same stream. Other studies have investigated the effect of controlling factors such as organic carbon, pH, and nitrogen inputs from non-native salmon runs (Strauss et al. 2002, Levi and Tank 2013). While there were no statistically significant relationships among nitrification rates and controlling factors in this study, there were trends, suggesting that more sampling could lead to more apparent relationships among the controlling factors and the nitrification rates. Nitrification is an extremely variable process due to the heterogeneous distribution of oxygen, ammonia, and bacteria across the streambed. Additionally, all sampling was completed in one season, autumn, making it potentially not representative of the full range of variation in a year. Other studies have looked at seasonal variation and found that increasing temperature in the summer months inhibited nitrification in coastal areas by favoring heterotrophs, which outcompete the nitrifying bacteria for ammonia (Hansen et al. 1981).

4.3 Implications for Other Streams with Dams

In the Messalonskee Stream, the five dams are inhibiting nitrogen transformations by increasing the flow of water. The fast flows reduce sediment deposition, which limits nitrogen transformations carried out by microbes in the sediment. This results in constant concentrations of ammonia and nitrate throughout the whole stream without much transformation between the two forms. The middle portion of the stream that does not have dams on it does have increased deposition and decomposition, however not enough nutrient cycling to effect the stream water nitrogen concentrations.

Additionally, the higher water level caused by reservoirs could play a role in inhibiting nitrification. Nitrification rates have been shown to have wide variation based on depth of water. Shallower areas (<2m) have shown to have significantly higher rates of nitrification than deeper sediments, and were deemed “hot spots” of N-transformation

(Bruesewitz et al. 2012). Dams create deep reservoirs out of previously shallower streams, potentially removing these essential hot spots of N-transformation, and reducing nitrification rates in the stream as a whole. Effects would be multiplied as the rapid flow below the dam erodes fine sediments to create a deeper channel below the dam as well. This can be seen from this study in case of Dam 4 where rates were below detection on both sides of the dam simply because there was not enough sediment substrate to support a colony of nitrifying bacteria.

The presence of a dam turns the stream into a pipe rather than a processor of nutrients. This is seen most drastically below dams where fast flows erode fine sediment, preventing any nutrient cycling from occurring there (Figure 12).

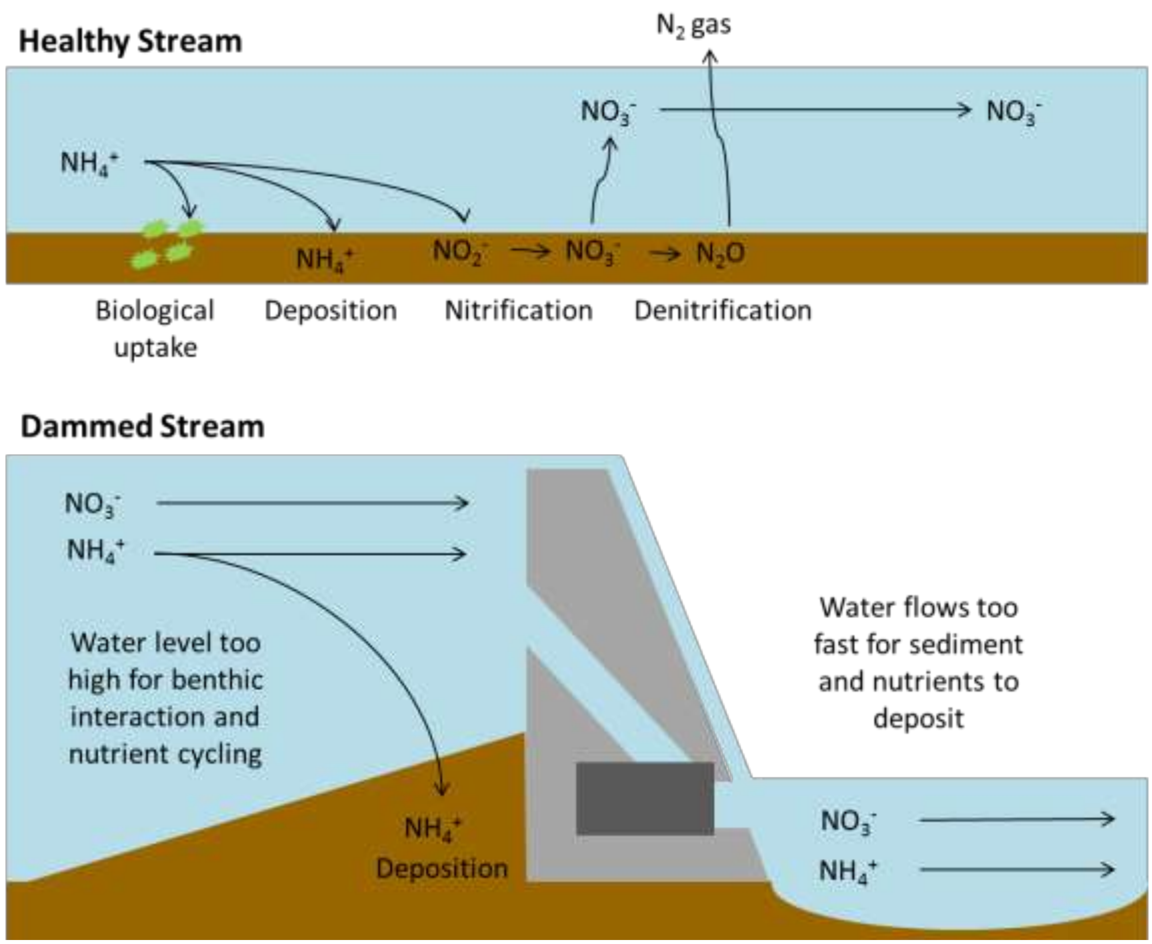


Figure 12. The impact of dams on nitrogen cycling compared to in a healthy stream.

Across the United States, there are over 75,000 dams ranging in size from under 5 to over 50 feet tall located on all sizes of streams from spring-fed headwaters to large continent-spanning rivers, often with several dams on one river system (Bednarek 2001). Dams, such as those on the Messalonskee Stream, exert control on a landscape scale by controlling the flow of the stream and the distribution of sediment within the channel. This will alter nutrient cycling and affect biological community health and structure. The combination of all of these factors is the ecological stability of the ecosystem, and in rivers, this ecosystem integrity depends on maintaining their dynamic character (Poff et al. 1997). A disturbance such as a dam which imposes limits on the system by controls flow rates and sediment distribution independently of natural factors, will compromise ecological integrity with multiple factors (Figure 13). Stream restoration must focus on the larger picture of stable stream ecosystems rather than just increasing fish passage.

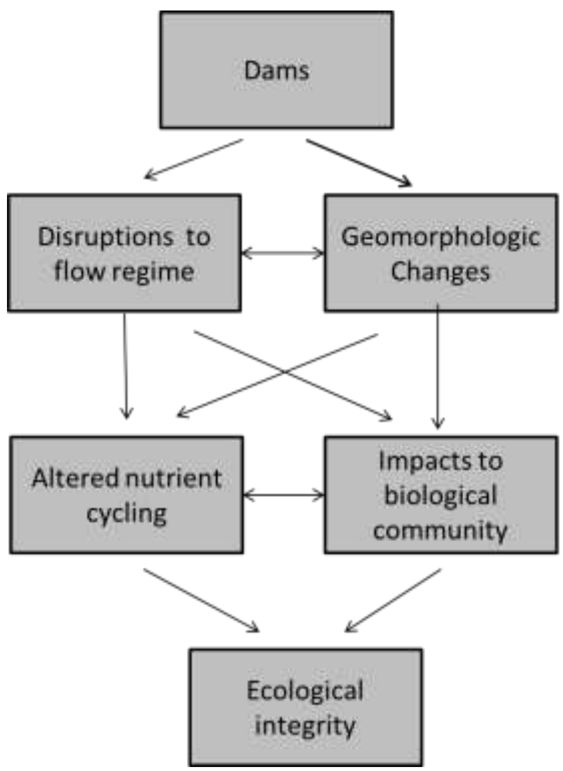


Figure 13. A summary diagram of the various interacting ways in which dams impair ecological integrity.

4.4 Alternative Pathways for Nitrogen Processing

One key question resulting from this study is where the riverine N is going, if the rates of processing in the stream benthos are so small. It is possible for the nitrification to move from the sediment and into the water column to be carried out by free-floating bacteria. Nitrification has been documented to occur in the water column of lakes suggesting that if the benthic habitat is not favorable to nitrification, the water column could be more suited it. This occurs under conditions of low nitrogen inputs, high N cycling rates, and strong N-limitation in the phytoplankton (Carini and Joye 2008). This is unlikely to be the case in the Messalonskee Stream because the observed nitrate concentrations were all below detection, and fast flows result in too short of a water residence time for much nitrogen cycling. Thus the likely scenario is that nitrogen inputs to Messalonskee Stream are not being process in the stream, and are just washed out to the Kennebec River to be cycled there.

It has been generally agreed that larger rivers are less efficient at cycling nutrients than smaller streams because there is a much larger volume of water for only a slightly larger benthos surface area creating less interaction between the water column and the benthos for nutrient cycling (Alexander 2000). However, recent tracer studies of larger rivers reveals that large rivers can just as effective for nitrogen uptake due to biological demand of the phytoplankton communities (Tank et al. 2008). No studies of nitrogen uptake or cycling have been done on the Kennebec River to see which of these theories is applicable. The Kennebec River still has several dams on it with one of them just upstream of the mouth of the Messalonskee Stream, making it possible the nitrification is inhibited by dams in the Kennebec as well. This would result in nitrogen washed to the coast at Merrymeeting Bay without returning to inland nutrient cycles.

4.5 Impacts of Nitrification Loss on Nitrogen Cycling as a Whole

A decrease in nitrification rates due to dams will decrease the mobility of nitrogen in the stream due NH_4^+ adsorbing onto sediment particles, as well as reduce the potential for denitrification. Denitrification not only is an important energy source for benthic bacteria, but it serves to remove nitrogen from a system to release it into the atmosphere as N_2 gas. This will decrease in-stream nitrogen cycling as a whole and increase nutrient

export to downstream water bodies. A loss of N-transformations makes the stream a pipe transporting water and solutes to the next water body and not a dynamic system where nutrients are used and by biota and retained in the ecosystem.

Future research is needed to elucidate the rates of denitrification and biological uptake compared to nitrification rates in the Messalonskee Stream as well as other streams with dams. If dams inhibited nitrification, it is likely that they will disrupt denitrification and biological uptake as well.

4.6 Management Solutions to Enhance In-stream Nitrogen Cycling

This study has revealed that the most significant way in which dams impact N-cycling is through creating exaggerated flow conditions that increase water retention and sediment erosion, creating a deeper channel on both sides of the dam. This deeper streambed reduces nitrogen transformations because it limits oxygen penetration into the sediment and lessens interactions between the water column and the benthos.

To increase in-stream nitrogen cycling, it is necessary to restore portions of habitat to shallower back-water pools and wetland-like ecosystems. These shallower areas will create hotspots of coupled nitrification and denitrification that will benefit the stream ecosystem as a whole by making nitrogen more available in all its forms in the ecosystem. Strauss et al (2004) found that nitrification rates were significantly higher in backwater areas than any other stream habitat. To create these areas, there must be periodic flushing of sediment that is caught in reservoirs above the dam, most notably above Dam 1. Allowing the sediment to travel to shallower areas where nitrification rates are higher, will allow for more in-stream nitrogen cycling as a whole.

Another solution is dam removal. The Union Gas Dam (Dam 5) on the Messalonskee Stream was removed when it washed out in 2001 and the stream was free-flowing for six years before the dam facility was sold and the dam rebuilt (Watt, personal communication). The water flow and sediment distribution as well as riparian and aquatic biota were observed to have returned to pre-dam conditions, but no studies were done of the effect of the dam removal on nutrient cycling. Ahern and Dahlgreen (2005) found that removal of a 3m tall dam on a creek in California increased concentrations of all nitrogen species below the dams as well as seasonal fluctuations based on changing

biological uptake. Dams, specifically older ones build for different economic conditions, must be evaluated for their effects on not only fish passage, but also nutrient transformations and geomorphologic structure, since these factors are so closely connected in a healthy, dynamic stream ecosystem.

CONCLUSION

The dams on the Messalonskee Stream act as a landscape-level control, defining distribution of sediment through the stream channel. This effects nitrification rates, but also likely has effects on denitrification, decomposition, as well as biotic communities. The combination of fast and variable flow causes the stream to act like a faucet flushing all the benthos, microbes, and nitrogen out to the Kennebec without processing it.

This study shows the impact that dams can have on stream ecosystems, even ones without a significant migratory fish population. In other studies as well, it has been found that geomorphological changes are the key to understanding long-term ecological consequences of dams and other stream disturbances because the form of the foundation for all other stream processes (Lignon et al. 1995). Except for Dam 5 which was replaced in 2007 all other dams are over 100 years old, at least twice as old as the 40-year average lifespan for a dam in the U.S. (Shuman 1995). And yet at least two of the five dams have recently been relicensed to remain for another 30 years (Watts, personal communication) There should be more research on effects of dam legacy and a focus on dam impacts at a watershed scale for not only biological reasons but also geomorphological. If the physical ecosystem foundation is compromised, than there is no way to restore biological integrity (Lignon et al. 1995) Managing dams at a basin scale allows for better balance between the economic demand for electrical power generation and ecological integrity of the stream or river system as a whole (Opperman et al. 2011). The lessons of dam assessment at a watershed scale learned from the Penobscot Restoration Project should be applied to the Messalonskee Stream and Kennebec River to work towards ecological stability of all of Maine’s flowing waters.

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