BEAVER AND MILL DAMS ALTER FRESHWATER MUSSEL HABITAT, GROWTH, AND SURVIVAL IN NORTH CAROLINA PIEDMONT STREAMS

A Thesis
by
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ABSTRACT

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Ecosystem engineers play an important role in the modification and partitioning of habitats and resources. In aquatic systems, anthropogenic and beaver (*Castor spp.*) dam building activities alter habitats and have profound effects on the availability, quality, and connectivity of resources and associated biotic communities. Freshwater mussels are imperiled indicator species, perform key ecosystem services, and serve as basal resources in stream foodwebs. Increasing beaver populations and mill dam removals may have consequences on freshwater mussel growth and survival. I examined the effects of beaver and mill dams on freshwater mussel resource availability and quality by measuring total suspended solid mass and carbon to nitrogen values. I complemented stream survey data with a juvenile mussel, common garden experiment conducted in the upper Tar River Basin of North Carolina, USA. I found that mill impoundments significantly improved mussel food quality, increased species richness, and growth of freshwater mussels in mill dam tailraces ($P < 0.05$). In contrast, mussels growing in streams with beaver impoundments did not experience elevated food resources or growth. Mussel mortality was twofold higher across all beaver reaches (39.9%) compared to mill reaches (20.0%). Patterns in mussel growth and survival were positively correlated with increased total suspended solid (TSS, <250 um) mass and %N, both measures of mussel food quantity and quality. My research shows that discontinuities in the flow continuum alter stream energetic pathways with dramatic consequences for the growth and survivorship of freshwater mussels. Increased water retention times resulting from impoundments may decrease nutrient spiraling lengths and increase nitrogen and small particle retention thereby increasing mussel food quality. Recently, advocates of wide-scale dam removals have suggested that removal of dams may improve habitat connectivity, but in nutrient-rich Piedmont streams dam removals may not be desirable as impoundments serve as important nutrient (including C) sinks. Quantifying costs and benefits of restored connectivity to taxa across multiple trophic levels as well as addressing effects on key small stream and wetland ecosystem services should be considered when prioritizing restoration projects.

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DEDICATION

I dedicate this thesis to my family and friends.

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FOREWORD

The body of this thesis will be submitted to *Ecology*, an international peer-reviewed journal owned by the Ecological Society of America; it has been formatted accordingly.

INTRODUCTION

Ecosystem engineers alter community function and structure through manipulation of resources and habitat availability (Jones et al. 1994, Wright and Jones 2006). Jones and colleagues (1994, 1997) first defined two main types of ecosystem engineering: (1) autogenic engineers that change the environment by their physical structures and (2) allogenic engineers that alter the physical state of the environment through manipulation of biotic and abiotic materials. Both autogenic and allogenic engineers are known from North American freshwater ecosystems; however, few studies have examined interactions between autogenic and allogenic engineers in these systems.

North American beaver, *Castor canadensis*, are well-studied allogenic ecosystem engineers (Collen and Gibson 2001, Wright 2009). Beaver modify lotic habitats and ecosystem processes through the removal of riparian vegetation and dam building activities. Newly formed impoundments significantly alter hydrologic regimes which lead to subsequent changes in energy and resource fluxes, specifically nutrient spiraling along the river continuum (Vannote et al. 1980, Naiman and Melillo 1984, Naiman 1988, Naiman et al. 1986, 1991, 1994). Beaver impoundments can improve aquifer recharge rates, entrain sediments, and increase hydrologic retention and net primary productivity (Gurnell, 1998, Collen and Gibson 2001, Rosell et al. 2005, Kemp et al. 2012). Specifically, dam construction increases watershed hydrologic retention capacity and ameliorates the severity of hydrograph peaks (Finnagan and Marshall 1997). Moreover, the size, watershed position, and age of the impoundment influence the degree of habitat alteration (McDowell and Naiman 1986, Fuller and Peckarsky 2011). Decreased canopy cover and increased pond surface area increases water temperature within the impoundment and downstream of the dam, while increasing thermal inertia (Cook 1940, Kemp et al. 2012). Newly constructed beaver impoundments increase stream acidity and pH. However, increases in sedimentation over time in older ponds result in higher acid-neutralizing capacity compared to adjacent free-flowing reaches (Cirmo and Driscoll 1993, Collen and Gibson 2001). Increased organic matter deposition and microbial decomposition rates lead to decreased dissolved oxygen level within impoundments (Naiman et al. 1994). For instance, Schlosser and Kallemeyn (2000) found that beaver impoundments were generally hypoxic with dissolved oxygen (DO) levels averaging <0.4 mg L^{-1}.

Beaver-induced hydrological changes govern key nutrient cycling pathways including anaerobic and aerobic decomposition. Specifically, beaver ponds alter carbon storage and turnover rates through increases in sediment and allochthonous inputs from inundated upland areas and the felling of trees (Ford and Naiman 1988, Naiman et al. 1994). In subarctic streams, nitrogen fixation can be 9 to 44 times greater in beaver-impoundment sediments when compared to free-flowing sections of the same stream (Francis et al. 1985). Several studies report a general increase in assimilatory carbon, nitrogen, and phosphorus levels in beaver impoundments (Collen and Gibson 2001). However, the degree of nutrient increase is dependent on impoundment size, stream velocity, and season (Fuller and Pekarsky 2011).

Freshwater mussels also act as ecosystem engineers. Recent evidence suggests that freshwater mussels engineer sediment microhabitats through the production of pseudofaeces (mucous packaged sediment which has not passed through the gut of the mollusk) (Vaughn et al. 2008). Mussels filter large quantities of water, removing sediment particles, algae, bacteria, and biodeposit faeces and pseudofaeces into sediments and stream flows, thereby increasing nutrient cycling rates. Additionally, shells of freshwater bivalves can alter current patterns in streams by turning soft sediments into complex substrate, and increasing friction at the surface of the substrate (Watters 1994, Allen and Vaughn 2011). The shells also provide shelter for many benthic invertebrates. Gutiérrez et al. (2003) found that freshwater mussels act as stable substrate, promoting colonization by epizoic invertebrates on the outside of their shell. Lastly, live mussels stabilize substrates and release sediment and mucous (pseudo-faeces), nutrients, and excrements, which encourages growth of invertebrates and algae (Beckett et al. 1996P, Vaughn and Hakenkamp 2001).

Anthropogenic dams alter landscape and ecosystem-level processes by transforming riverine habitats into lacustrine areas. The degree to which dams alter the transport and processing of organic matter, nutrients and sediment to downstream reaches, and restrict the movement of lotic organisms largely depends on dam size (Poff and Hart 2002). Large, hypolimnetic-releasing dams, such as hydropower dams, profoundly alter stream physicochemical habitat for substantial distances downstream (Baxter 1977, Watters 1996).

Several studies have examined the effects of large hydropower dams on freshwater mussel populations (Bates 1962, Suloway et al. 1981, Williams and Fuller 1992, Blalock and Sickel 1996, Vaughn and Taylor 1999). Vaughn and Taylor (1999) found that mussel species decreased with increasing linear distance from large-scale hypolimnetic dams and reservoirs. Mussels downstream of large scale impoundments are likely affected by hydrologic scouring, decreasing water temperatures, habitat shifts, food availability, and host-fish abundance (Vaughn and Taylor 1999).

More recently, studies have examined effects of low-head dams on freshwater mussels (Watters 1996, Dean et al. 2002, Tiemann et al. 2007, Singer and Gangloff 2011, Gangloff et al. 2011, McCormick 2012). Predictably, Dean et al. (2002) and Tiemann et al.

(2007) showed that impounded reaches of Kansas and Illinois streams had lower mussel abundance and richness when compared to free-flowing sites. However, other studies suggest that freshwater mussels in mill pond tailraces may benefit from impoundments (Gangloff et al. 2011, Singer and Gangloff 2011). Alabama streams with intact mill dams had significantly higher mussel catch per unit effort (CPUE) and species richness compared to streams with breached or relict dams (Gangloff et al. 2011). Recent research in North Carolina showed similar results (McCormick 2012). Preliminary research suggests that low-head dams increase streambed stability, mussel food quality, and temperature resulting in elevated mussel growth rates immediately below the dam (Singer and Gangloff 2011). Moreover, smaller anthropogenic dams (e.g., mill dams) have hydrologic and biogeochemical attributes that are analogous to beaver impoundments (Francis et al. 1985).

Both mill and beaver dams affect aquatic communities. Beyond their obvious effects on plant communities, beaver dams have significant effects on fish and macroinvertebrate community composition (McDowell and Naiman 1986, Naiman et al. 1988, Gurnell, 1998, Collen and Gibson 2001). McDowell and Naiman (1986) found increased aquatic invertebrate biomass associated with changes in particle size, organic matter concentration and carbon and nitrogen ratios in beaver-affected reaches. Analysis of coarse particulate organic matter (CPOM), fine particulate organic matter (FPOM), and very fine particulate organic matter (VPOM) showed positive correlations with invertebrate densities and biomass (McDowell and Naiman 1986). Specifically, beaver impoundments increase decomposition and carbon export rates which elevate biomass and densities of aquatic invertebrates in downstream reaches (McDowell and Naiman 1986). Fuller and Peckarsky (2011) observed increases in suspension feeding invertebrates downstream of beaver impoundment when compared to upstream reaches, with the highest densities occurring downstream of deeper impoundments with higher head height.

Beaver-dam-induced alteration of nutrient cycling regimes, water chemistry, and host-fish movement may be contributing to range declines of endangered freshwater mussels in highly-stressed southeastern US Piedmont streams (Woodward et al. 1985). How particle size, organic matter, and suspended particulate carbon to nitrogen (C:N) ratios vary as a result of beaver activity and their effect on less mobile, long lived aquatic invertebrates like freshwater mussels is unclear. Few prior studies have examined effects of beavers on freshwater mussels (Rudizte 2005). Disparate effects of beaver and mill dams may result in distinct changes to ecosystem processes, including nutrient retention and cycling rates.

Freshwater mussels play a critical role in North American lotic and estuarine ecosystems as filter feeders, primary consumers, and detritivores (Poole and Downing 2004, Vaughn and Hakenkamp 2001, Haag 2012). Presently, 301 species of freshwater mussels are recognized in the United States (Families Margaritiferidae and Unionidae), with 213 (71%) of those taxa considered endangered, threatened, or of special concern (Williams et al. 1993, Ricciardi and Rasmussen 1999, Watters 2001, Bogan and Roe 2008, Williams et al. 2008). North Carolina is experiencing one of the highest rates of freshwater mussel decline and current estimates suggest that 59% (29 spp.) of native unionid fauna are extinct or at-risk of becoming extinct (Neves et al. 1997, Bogan 2007, Haag 2010). The rapid decline of freshwater mussels in North America and worldwide in the past five decades is attributed to increased frequency of large, habitat fragmenting and altering impoundments, effects of at least three highly invasive bivalves, land-clearing and channelization that lead to increased siltation and channel geomorphic alteration (Williams et al. 1998, Strayer et al. 2004, Strayer and Malcom 2007). The alarming rate of mussel species loss is of great concern because it foretells losses in other more mobile or less sensitive groups (i.e. fishes, crayfish, insects). Dramatic losses to North America's freshwater diversity demand a need for a more holistic and experimentally-based understanding of how ecological mechanisms exacerbate or mitigate human impacts and affect sensitive taxa including freshwater mussels.

My study explores the complex interactions between three ubiquitous stream ecosystem engineers: beavers, humans, and freshwater mussels. The objectives of this study are to: 1) explore how beaver and mill dams affect mussel habitat, food quantity, and food quality by measuring shift in habitat (depth, flow, substrate, dissolved oxygen etc.), carbon and nitrogen ratios (C:N) and mass of total suspended solid (TSS) and 2) examine changes in mussel growth between beaver and mill dam reaches by conducting mussel surveys and a common garden experiment using endemic captive-reared juvenile mussels. I predict that higher retention times and increased organic matter inputs in beaver and mill impoundments will increase nutrient availability (TSS mass) and quality (TSS C:N) when compared to up and downstream reaches. In contrast, I predict that mill ponds and tailraces will have higher quality food resources than do beaver dams because deeper, more permanent mill ponds will increase resource quality (high amounts of autochthonous resources and lower C:N). Because mill dams are more permanent structures with lower levels of disturbance, I predict that mussel CPUE, richness, growth, and survival will be greatest below beaver and mill dams when compared to control reaches, with mill dams having the highest growth, density, and diversity of mussels.

MATERIALS AND METHODS

Study Area

Study streams were located ~70 km north of Raleigh, North Carolina in the upper Tar River Basin (Fig. 1). All study streams are 2nd to 4th order headwaters draining small, forested and agricultural piedmont catchments. One site was located on the mainstem Tar River and five sites on Tar River tributaries: Fishing, Shocco, Shelton and Sandy (2 sites) creeks. Fishing, Shelton and Shocco creeks are designated as sensitive waters (i.e., streams supporting federally-listed fish or mussels) by the North Carolina Wildlife Resources Commission (NCWRC). Beaver and two federally endangered mussels *Alasmidonta heterodon,* (Dwarf wedgemussel- DWM) and *Elliptio steinstansana* (Tar River spiny mussel- TRSM, Rob Nichols, NCWRC pers. com.) co-occur in these streams.

McCormick (2012) sampled mussels and habitats at reaches associated with the three mill dams, and I sampled mussels and habitats at the three beaver dams. Laurel Mill Dam was constructed on lower Sandy Creek northeast of Louisburg in Franklin County, NC, and is on the National Registry of Historic Places. Hamme's Mill Dam is located on Fishing Creek southwest of Warrenton in Warren County. Gooch’s Mill was constructed in 1797 on the Tar River in Granville County, NC. For each mill dam site, I selected four 150-m reaches: (1) an upstream reference reach located at least 500 m upstream from the impoundment and 0-2.0 km upstream of the dam, (2) the mill pond, (3) the mill dam tailrace located 0-150 m downstream from the dam, and (4) a downstream reach located 500-650 m downstream from the dam. For beaver sites, I selected four study reaches: (1) an upstream reference reach located at least 500 m upstream from the impoundment and 0-5.0 km upstream of the dam, (2) the impoundment, 0-200 m upstream of the focal dam, (3) the beaver tailrace, ~ 0-150 m downstream from the most recently-maintained dam in the beaver dam complex, and (4) a downstream reach, 500-650 m downstream of the focal beaver dam. Upstream reaches of both mill and beaver dam sites serve as reference reaches and all six have no apparent signs of either beaver activity or mill dam construction.

Total Suspended Solids

I measured depth, velocity (m/s), dissolved oxygen (DO) (% saturation, mg/L), temperature, conductivity, specific conductance and pH at each reach. I collected three replicate 4-L, mid-column water samples from each reach during winter, spring, and summer of 2012 for analysis of total suspended solids (TSS). Vaughn and Hakenkamp (2001) showed that mussels feed primarily on <250-µm particulates. Therefore, water was filtered *in vivo* through a 250-µm sieve and stored on ice in 10% HCl acid-washed Nalgene bottles until filtered. Water samples were vacuum-filtered through pre-ashed (500°C for 1 h) and pre-weighed 47 mm Gelman™ type A/E 1.0 µm pore glass fiber filters (GFF). If filters clogged before reaching 4 L, I used the final volume of filtered water for calculations, although no more than 100 mL of sample was poured at each time to prevent clogging. Filtered samples were immediately frozen (-20°C) and then lyophilized. To quantify TSS quantity and quality, GFF and TSS were weighed and analyzed for carbon to nitrogen analysis with a Thermo Scientific Flash EA 1200 combustion analyzer (Appalachian State University, Boone, NC, USA). Three blank GFF's were prepared and analyzed as controls using the same protocols.

Mussel Surveys and Habitat Measurements

I performed timed mussel surveys and quantified mussel density and stream physico-chemical habitat parameters at upstream, tailrace, and downstream reaches. Reaches were divided into 16 transects, spaced 10 m apart. I placed five 0.25 m^2 quadrats along each transect and carefully excavated each quadrat by hand to a depth of 10 cm. I identified all mussels to species and measured maximum length (± 0.1 mm) of all individuals (or a random subset when mussels were hyper-abundant) using calipers. Threatened, endangered and special concern mussels were quickly measured and returned to their original positions.

Temperature was monitored continuously for one year using NexSens temperature loggers (NexSens Technology, Inc., Fairborn, OH) anchored to the streambed. I quantified stream habitat (e.g., depth, flow, distance to bank, and substrate n = 12 particles) within each quadrat.

Mussel Propagation

I studied *Lampsilis radiata* (Gmelin, 1791), a common and widespread freshwater mussel that occurs from Maine to Georgia in Atlantic Slope drainages (Johnson 1970). Two gravid females were collected from a high density *L. radiata* population in Shelton Creek, Granville County on February 4, 2011. Mussels were transported to the Aquatic Epidemiology and Conservation Center (AECC) at North Carolina State University. I extracted glochidia from one gill per mussel by inserting a water-filled syringe into the marsupium and infested 100 quarantined fingerling *Micropterus salmoides* (Foster Lake Pond Management, Raleigh, NC, USA) with 96,000 glochidia in 12 L of water for eight minutes. Two weeks after infestation, I collected and transferred juvenile mussels to down-welling systems (Barnhart 2006). Mussels were fed a mixture of live, cultured algae

(*Oocystis polymorpha*) and commercially available algal products (*Nannochloropsis, Isochrysis*, *Pavlova, Tetraselmis*, and *Thalassiosira weissflogii* from Reed Mariculture Inc., Campbell, CA) at a concentration of 50-100,000 cells/mL (Barnhart 2006).

When juveniles reached a mean size of 1.5 mm, I transported them from the AECC to the North Carolina Wildlife Resources Commission's Marion Conservation Aquaculture Center (MCAC) in Marion, NC. Juvenile mussels remained in 26.5 L flow-through growth chambers with sand substrate (<1 mm) and a constant supply of hatchery pond water. At a mean length of 4 mm, I transferred mussels from the growth chambers to 19-L air-driven upwellers suspended 0.3 m from the surface of the pond. Upwellers were cleaned bi-weekly and remained in the pond until October 2011 when mussels were placed back into 26.5-L growth chambers until the beginning of December 2011. I tagged each mussel with unique bee tags (Queen Marking Kits, The Bee Works, Orillia, ON, Canada) on the umbo (dorsal) region using Zap-a-Gap adhesive (Pacer Technology, Rancho Cucamonga, CA, USA). In December 2011 after nine months of growth, I transported juvenile mussels in aerated coolers to the field for deployment. A subset of mussels (*n* = 15) were transported to the field and returned to the hatchery to serve as handling controls.

Juvenile Survivorship Field Study

I placed five propagated *Lampsilis radiata* juveniles in each of three 18(W) x 18(L) x 10(H) cm plastic mesh cages at each reach along with ~5 cm of reach-specific substrate. I constructed cages using fine (2 mm) and coarse (10 mm) photoresistant plastic mesh and closed them with cable ties and 100% silicone. I anchored cages in the stream using 0.64 cm x 61 cm rebar and cable ties (Gangloff et al. 2009). I placed three cages in each reach (*n* =15 mussels per site, 45 per dam). I checked cages every two months and removed debris. I recorded mussel length (widest anterior to posterior distance, ± 0.1 mm), wet weight (± 0.01 g), cage depth, and mid-channel velocity seasonally (Feb, May, Aug, Oct. 2012). In October, I removed mussels from cages took final length and weight measurements and placed them in a -80°C freezer for long term storage. I quantified substrate within cages at the end of the experiment by categorizing 20 randomly selected particles as wood, organic, sand, silt, clay, or measured particles (>2 mm). I measured all particles >2 mm along the greatest width.

Statistical Analyses

I analyzed all data using SPSS (ver. 20; SPSS, Inc. Chicago, IL). I used X^2 analyses to assess if mortality varied by dam type (beaver or mill dam) and reach.

I tested whether mussel growth rate was influenced by treatment (dam type) and reach using a repeated measures linear mixed model. My repeated measure was individual mussel length (mm) with mussel ID as the subject. Fixed effects were: season (spring, summer, fall), treatment (mill dam versus beaver dam), and reach (upstream, impoundment, dam, and downstream). My random effect was cage number. I found significant interactions between season, treatment, and reach so I split the data by season and treatment and performed subsequent analyses by testing for differences in growth among reaches within each season and treatment.

I tested for differences in mussel food quantity (TSS mg/L) and quality (TSS %N, %C, and C:N) using 3-way ANOVA. Fixed effects were treatment, season, and reach. I detected significant interactions between all fixed factors so I split the data by season and focused on the time period of highest mussel growth (summer). I found significant interactions between treatment and reach during the summer so I again split the data and performed subsequent analyses testing for differences among reaches within the same treatment and season.

In order to assess the influence of important habitat parameters on mussel growth, I constructed a backwards stepwise multiple regression. I included site scale mean velocity (m/s), temperature, pH, specific conductance, DO (% saturation), particle size (mm), percent fine substrates (sand, slit, clay), TSS, % C (adjusted for sample weight), % nitrogen (adjusted for sample weight) and C:N as predictor variables with change in length (mm) as the dependent variable.

RESULTS

Mussel Mortality and Growth

Total mussel mortality was significantly higher in beaver streams (39.3%) compared to mill streams (20.0%; Pearson's $X^2_1 = 15.56$, $P < 0.001$; Table 1). Moreover, mortality varied with reach. Mussel mortality was highest at impoundments (48.1%) compared to all other reaches (US: 25.6%, Dam: 24.7%, DS: 22.3%; Pearson's $X^2_3 = 17.04$, $P < 0.001$; Table 1). Patterns of mortality across reaches varied with treatment. In stream with beaver dams, mortality was highest at impoundments (68.6%) compared to other reaches (US: 13.6%, Dam: 43.2%, DS: 38.0%; Pearson's $X^2_3 = 25.03$, $P < 0.001$; Table 1). Streams with mill dams showed opposite patterns in mortality with the highest mortality rates occurring at upstream and impoundment reaches (38.1%, 31.8% respectively) and the lowest rates occurring at dam and downstream reaches (6.7%, 4.5% respectively, Pearson's $X^2_3 = 24.0$, $P < 0.001$; Table 1). Predation and handling errors resulted in a 5% ($n = 17$) loss of the total sample.

Repeated measures mixed model analyses showed a highly significant interaction between treatment and reach ($F_{3,63.3} = 6.812$, $P < 0.001$). Cage had a significant effect between reaches but not among reaches within the same treatment (Wald Z = 3.055, $P < 0.05$). All mussels grew at different rates between seasons with the highest growth rates occurring in the summer (Table 2, 3; Figs 2, 3, 4). In streams with mill dams, mussels grew faster at dam reaches when compared to other mill reaches (Table 2; Fig. 2). However in streams with beaver dams, mussel growth did not differ significantly among reaches (Table 2; Fig. 3). Moreover, mussels within the same reach varied in growth between mill dam and beaver dam streams. Mussels upstream of beaver impoundments grew faster than mussels upstream from mill ponds but mussels in beaver impoundments and tailraces grew significantly slower than mussels in analogous mill pond reaches (Table 3). No significant difference in growth occurred at downstream mill and beaver reaches (Table 3).

Habitat and Food Measurements

Habitat parameters varied strongly with season. Mussel growth was highest during summer so I focused on relationships between growth and summer habitat parameters. Temperature, specific conductance, percent DO saturation, velocity (m/s), and substrate (% fine and mean particle size) were not significantly different between treatments or among reaches (Table 4). However, mean dissolved oxygen (%) tended to be lower in beaver impoundments compared to up- and downstream reaches and corresponding mill reaches with minimum observed values consistently below 30% from spring to fall (Fig. 5). Total suspended solid concentrations were significantly higher in beaver reaches than mill reaches ($P < 0.05$; Table 5; Fig. 6). Total suspended solid C:N was higher in beaver tailraces (10.74 ± 2.43 SE) compared to mill tailraces (9.20 ± 1.68 SE; Table 5; Fig. 7). Impoundments produced significantly higher % N adjusted (adjusted for the % of the sample that was TSS versus GFF) when compared to all other reaches (Fig. 8). Upstream reaches had the lowest N levels but were not significantly different from downstream reaches. Dam reaches had higher % N adjusted than upstream reaches, but lower nitrogen levels than did impoundments (Fig. 8).

Across treatments, streams with mill dams had higher %N than did beaver dams (Table 5). Percent C (adjusted for the % sample that was TSS versus GFF) varied between treatment and reach (Table 5). Moreover, only upstream reaches significantly differed in % C adjusted between beaver and mill treatments, with beaver reaches having higher % C adjusted (Fig. 9). Impoundments had higher % C compared to up and downstream reaches, but did not significantly differ from dam reaches (Fig. 9). Dam reaches had significantly higher % C adjusted than upstream and downstream reaches. Downstream reaches had % C levels similar to upstream and tailrace reaches but lower levels than impoundments.

Mussel Field Surveys

Mussel CPUE and total species richness varied significantly between streams with beaver and mill dams but were not significantly different between reaches (Tables 6, 7; Fig. 10). CPUE was highest in streams with mill dams and lowest in streams with beaver dams. Mill tailraces had the highest mussel CPUE and CPUE was lowest upstream of beaver impoundments. Mussel density in streams with beaver dams was not significantly different among reaches (Table 6).

Predictors of Mussel Growth

Mean % N, pH, and TSS mass were significant predictors of mussel change in length ($\beta = 0.87$, $\beta = 0.39$, $\beta = 0.40$, respectively). Mussels in reaches with higher pH, TSS, and % N exhibited faster growth compared to mussels in reaches with lower pH, TSS and %N ($R^2 = 0.54$, $F_{3,16} = 7.29$, $P = 0.004$; Fig. 11).

DISCUSSION

My results suggest that mill dams positively affect mussel growth and survival whereas beaver dams negatively affect mussel survival but not growth. Juvenile freshwater mussels in mill tailraces grew significantly faster than mussels up- or downstream of the dam. However, mussels located near beaver dams did not exhibit significantly different growth patterns. Additionally, mussel mortality was 2 times greater in streams with beaver impoundments compared to streams with mill dams. Beaver-created wetlands are dynamic systems (Collen and Gibson 2001, Kemp et al. 2012). Frequent changes in flow, temperature, and food resources may negatively affect mussel survival and growth. Although not significantly different from mill impoundments, mean dissolved oxygen levels in beaver impoundments tended to be lower and may also inhibit the feeding rates and growth of freshwater mussels. Stream total wetted-width and flow changed dramatically between seasons in streams affected by beavers. During the course of the study, three new beaver dams were constructed and washed out within study reaches. Receding water levels exposed several cages in beaver impoundments and tailraces. In contrast, mill dam tailraces offered more stable environments with higher quality food, higher dissolved oxygen levels, relatively constant depth, and velocity regimes compared to beaver dam tailraces.

Changes in food quality and quantity may cause freshwater mussel to switch feeding behaviors. Vaughn et al. (2008) documented freshwater mussels engaging in three different types of feeding behaviors: 1) filter feeding 2) deposit feeding and 3) pedal feeding. Mussels tend to shift between feeding types based on age and relative food abundance and quality. Additionally, mussels can shift the type of food consumed based on resource availability (Vaughn and Hakenhamp 2001). Freshwater mussels consume phytoplankton, bacteria, algae, detritus, and dissolved organic matter (DOM) (Vaughn et al. 2008). For example, Singer and Gangloff (2011) found that elevated food quality may partially explain increased mussel growth downstream from some small impoundments.

Mussel growth and habitat data suggest that mill dams likely influence mussel growth by altering TSS C:N ratios. TSS and deposited organic matter are likely the primary food sources for freshwater mussels in these streams. Mill dams enhance the quality of mussel food via enhanced autotrophy and significant increases in % N within mill impoundment and tailrace TSS. Beaver dams increased TSS quality within both impoundments and tailraces but C:N was higher in beaver than in mill dam impoundments suggesting poorer food quality in beaver dam reaches. TSS levels were highly variable in beaver-affected streams yet relatively constant in mill reaches further suggesting that constant beaver activity may cause dramatic and acute shifts in the concentration and quality of TSS. This likely has an important effect on the quantity and quality of mussel food resources which could influence mussel growth. Although mill dams export lower levels of higher-quality TSS relative to beaver dams, intra and inter-annual variability in TSS export and quality are much higher in beaver dam-affected streams. This may be why mussels appear to respond less strongly to beaver impoundment-mediated alteration of food quality than they do to changes associated with more temporally and hydrologically stable human-constructed dams.

Impounded stream reaches and large pools in un-impounded streams may be important sources of high-quality seston for filter-feeders. For example, during periods of low flow, Ichawaynochaway Creek in south-central Georgia produced seston with lower C:N, less depleted $\delta^{13}C$, and higher $\delta^{15}N$ compared to seston produced during higher water periods (Atkinson et al. 2009). Because smaller particles harbor higher bacterial biomass (relative to volume), the food quality of smaller seston particles is generally greater than larger particles (Kondratieff and Simmons 1985, Edwards 1987, Kamauchi 2005, Atkinson et al. 2009). Singer and Gangloff (2011) showed that the inorganic: organic ratio of TSS exported from a mill dam was significantly higher within impoundments and mill tailraces during the spring when compared to up-and downstream reaches. Moreover, mussels inhabiting the tailrace were significantly larger when compared to mussels of the same age from up- and downstream reaches. Therefore, increased O:I downstream of small mill ponds may drive faster mussel growth rates. My data show similar patterns with the highest mussel growth occurring in reaches with low C:N values and high %N of TSS. Additionally, increased %N in TSS within mill ponds and downstream from dams suggests that mill impoundments and dams have higher quality food resources and conditions that should lead to faster bivalve growth rates (Sterner and Elser 2002).

The river continuum concept states that nutrient cycling is driven by the hydrology and productivity of river systems (Vannote et al. 1980). My research shows that discontinuities in the flow continuum alter stream energetic pathways with dramatic consequences for the growth and survivorship of threatened freshwater invertebrates. Higher retention times resulting from impoundments may decrease nutrient spiraling rates, increasing nitrogen and small particle retention. Seston quality is positively correlated with residence time (Hoffman 2005). Therefore, high-quality TSS exported from mill dams may be the result of increased retention times in mill impoundments. Surveys of North Carolina mill dams (including the dams studied here) revealed higher mussel density, CPUE and larger mean mussel lengths in mill dam tailraces. Specifically, *Elliptio complanata*, the numerically dominant mussel in many Atlantic Slope streams, are larger below intact dams (McCormick 2012).

Implications of study

North Carolina is experiencing large-scale declines in federally and state listed mussel species. Populations of two endangered mussels, *Alasmidonta heterodon* and *Alasmidonta raveneliana*, have undergone sharp declines within the last decade (NCWRC). Contributing factors to species losses include changes in landuse, decreases in water quality, and invasive species (Strayer et al. 2004). Increasing interest in stream restoration and mitigation has spurred numerous dam removals across the state of North Carolina and many are being planned. My research has important implications for the prioritization and removal of dams. Specifically, my results suggest that mill dams increase mussel growth through increases in food quality and may therefore have value as conservation-enhancing structures. Additionally, dams may sequester pollutants from changes in landuse and reduce high sedimentation and eutrophication downstream. Therefore, dam prioritization should incorporate both the short and long term costs and benefits associated with dam removal.

Beaver populations have made a remarkable recovery from near extinction. Beaver numbers in North America are estimated to be between 6 to 12 million individuals (Naiman et al. 1986). Historically, beavers coexisted with freshwater mussels prior to European settlement. However, modern streams may not resemble pre-European streams due to dramatic changes in landuse and stream hydrology. As a result, the impoundments created by beaver today may have different implications for mussel survival and growth. My study suggests that beaver dams increase mussel food quality, but the low dissolved oxygen levels and dynamic changes in habitat causes high mortality in *Lampsilis radiata*. Therefore, expanding populations of beavers may threaten remaining known populations of federally endangered mussels in North Carolina (NCWRC) and require removal or management in areas of overlap with mussel species of high conservation concern. However, further research is needed to understand how beaver dams affect different species of freshwater mussels.

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TABLES

Table 1
Total number of mussels alive and dead and change in length of living mussels

	Alive (n)	**Dead (n)**	**Total (n)**	**Mortality (%)**	**Change in Length (mm) (mean ± SE)**
Beaver	105	68	173	39.3	6.2 ± 0.3
Upstream	38	6	44	13.6	8.9 ± 0.4
Impoundment	11	24	35	68.6	2.4 ± 0.3
Dam	25	19	44	43.2	5.1 ± 0.4
Downstream	31	19	50	38.0	6.1 ± 0.6
Mill	140	35	175	20.0	7.2 ± 0.3
Upstream	26	16	42	38.1	3.3 ± 0.2
Impoundment	30	14	44	31.8	7.0 ± 0.4
Dam	42	3	45	6.7	11.2 ± 0.7
Downstream	42	2	44	4.5	5.8 ± 0.3

Table 2

Repeated Measures Mixed Model analysis testing the effects of reach and season on mussel length (mm) within the same treatment

Treatment	**Factor**	**df**	**Estimate (SE)**	***F***	***P*-value**
Beaver	*Reaches*	*3,32.825*		*1.88*	*0.152*
	Upstream		0.65 ± 0.54[a]		
	Impoundment		0.08 ± 0.57 [a]		
	Dam		-0.67 ± 0.55[a]		
	Season	*3, 195.26*		*78.20*	*< 0.001*
	Winter		-6.46 ± 0.48 [b]		
	Spring		-5.27 ± 0.48 [b]		
	Summer		-1.72 ± 0.57 [b]		
Mill	*Reaches*	*3, 30.33*		*5.522*	*0.04*
	Upstream		-1.45 ± 0.66[c]		
	Impoundment		0.55 ± 0.66 [c]		
	Dam		1.11 ± 0.65 [c]		
	Season	*3, 230.03*	*230.031*	*142.32*	*< 0.001*
	Winter		-7.53 ± 0.42 [b]		
	Spring		-5.79 ± 0.43 [b]		
	Summer		-1.84 ± 0.45 [b]		

a. Estimates relative to downstream beaver lengths (downstream set to zero)
b. Estimates relative to fall length (fall set to zero)
c. Estimates relative to downstream mill lengths (downstream set to zero)

Table 3
Repeated Measures Mixed Model analysis testing the effects of season and treatment on mussel length within reach

Reach	**Factor**	**df**	**Estimate (SE)**	**F**	***P*-value**
Upstream	Beaver	1, 15.37	1.28 ± 0.60[a]	4.61	0.048
	Winter	3, 112.84	-6.36 ± 0.6[b]	47.47	< 0.001
	Spring		-4.66± 0.61[b]		
	Summer		-1.66± 0.65[b]		
Impoundment	Beaver	1, 15.31	-1.31 ± 0.47[a]	7.95	0.013
	Winter	3, 85.73	-6.55±0.62[b]	53.32	< 0.001
	Spring		-5.95 ± 0.63[b]		
	Summer		-1.03 ± 0.74[b]		
Dam	Beaver	1, 14.69	-2.27 ± 0.76 [a]	8.90	0.009
	Winter	3, 103.97	-9.00 ± 0.69[b]	74.88	< 0.001
	Spring		-7.34 ± 0.69[b]		
	Summer		-2.61 ± 0.76[b]		
Downstream	Beaver	1, 17.14	-.96 ± 0.57 [a]	2.87	0.109
	Winter	3, 134.68	-6.35 ± 0.55[b]	53.23	< 0.001
	Spring		-4.43 ± 0.55[b]		
	Summer		-1.56 ± 0.61[b]		

a. Estimates relative to mill (mill set to zero)
b. Estimates relative to fall (fall set to zero)

Table 4
ANOVA’s testing the effect of treatment and reach on select habitat parameters

Dependent Variables	**Factors**	**df**	**F**	***P***
Temperature (C)	Treatment	1, 23	0.046	0.833
	Reach	3, 23	1.461	0.263
	Interaction	3, 23	0.310	0.818
Specific Conductance	Treatment	1, 22	3.264	0.091
	Reach	3, 22	0.236	0.870
	Interaction	3, 22	0.186	0.904
DO (%)	Treatment	1, 22	0.128	0.726
	Reach	3, 15	0.674	0.581
	Interaction	3, 15	0.644	0.599
Velocity (m/sec)	Treatment	1, 22	0.030	0.864
	Reach	3, 22	1.787	0.193
	Interaction	3, 22	0.165	0.918
Fine Substrate (%)	Treatment	1, 17	2.263	0.158
	Reach	2, 17	1.307	0.307
	Interaction	2, 17	0.386	0.688
Mean Particle Size (mm)	Treatment	1, 17	2.737	0.124
	Reach	2, 17	0.484	0.628
	Interaction	2, 17	1.237	0.325

* Significant difference $P < 0.05$

Table 5
ANOVA's testing the effect of treatment and reach on food quality and quantity variables

Dependent Variables	**Factors**	**df**	**F**	***P***
TSS (mg/L)	Treatment	1, 23	6.283	0.023*
	Reach	3, 23	0.274	0.843
	Interaction	3, 23	0.035	0.991
C:N	Treatment	1, 23	3.613	0.076
	Reach	3, 23	0.648	0.596
	Interaction	3, 23	2.026	0.151
% C adj	Treatment	1, 23	6.946	0.018*
	Reach	3, 23	10.999	0.000*
	Interaction	3, 23	1.670	0.213
% N adj	Treatment	1, 23	9.782	0.006*
	Reach	3, 23	8.143	0.002*
	Interaction	3, 23	0.281	0.838

* Significant difference $P < 0.05$

Table 6
ANOVA's testing the effect of treatment and reach on mussel CPUE, density, and SR

Dependent Variables	**Factors**	**df**	**F**	***P***
CPUE	Treatment	1, 17	8.618	0.012*
	Reach	2, 17	1.157	0.347
	Interaction	2, 17	1.207	0.333
Density	Treatment	1, 17	4.146	0.064
	Reach	2, 17	1.303	0.307
	Interaction	2, 17	2.746	0.104
Species Richness	Treatment	1, 17	14.754	0.002*
	Reach	2, 17	2.123	0.162
	Interaction	2, 17	0.228	0.799

* Significant difference $P < 0.05$

Table 7

Reach scale mussel species richness (SR) and abundance

	Mill									Beaver								
	Gooch’s			**Hamme's**			**Laurel**			**Sandy**			**Shelton**			**Shocco**		
Mussel Taxa	**Up**	**Dam**	**DS**	**Up**	**Dam**	**DS**	**Up**	**Dam**	**DS**	**Up**	**Dam**	**DS**	**Up**	**Dam**	**DS**	**Up**	**Dam**	**DS**
A. heterodon															1		1	
E. complanata	328	411	374	72	652	559	590	351	205	181	49	52		36	463	6	143	396
E. congarea					3	3		1										
E. icterina	26	12	15		129	91	30	34	5	7	2	27		19	13			
E. lanceolata						5												
E. mediocris		4	1		12	34												
E. roanokensis	2	4			20	7		2										
Elliptio sp.	1405	870	392		4349	728	41	546	1									
E. viridulus			1	3	7	9												
F. masoni	7					1	1	1										
Lampsilis radiata	37	1			2			1						3	138			
S. undulatus		1													1			
V. constricta	3						1	1							3			
Species Richness	**7**	**7**	**5**	**2**	**8**	**9**	**5**	**8**	**3**	**2**	**2**	**2**	**0**	**3**	**6**	**1**	**2**	**1**
Total mussels	**1808**	**1303**	**783**	**75**	**5174**	**1437**	**663**	**937**	**211**	**188**	**51**	**79**	**0**	**58**	**619**	**6**	**144**	**396**

FIGURES

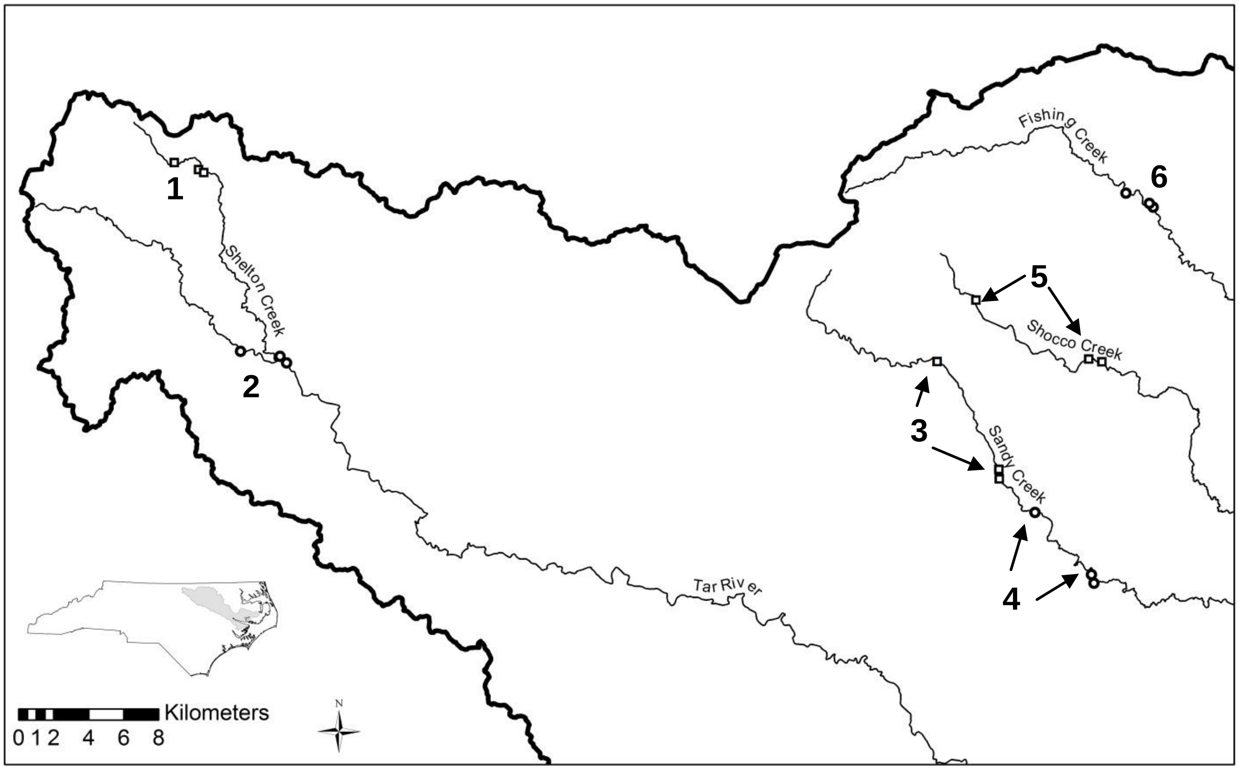

Figure 1. Map of study sites within the upper Tar River Basin. Squares represent beaver reaches and circles represent mill reaches. (1) Shelton Creek beaver reaches, (2) Gooch's Mill reaches, (3) Sandy Creek beaver reaches, (4) Laurel Mill reaches, (5) Shocco Creek beaver reaches, and (6) Hamme's Mill reaches.

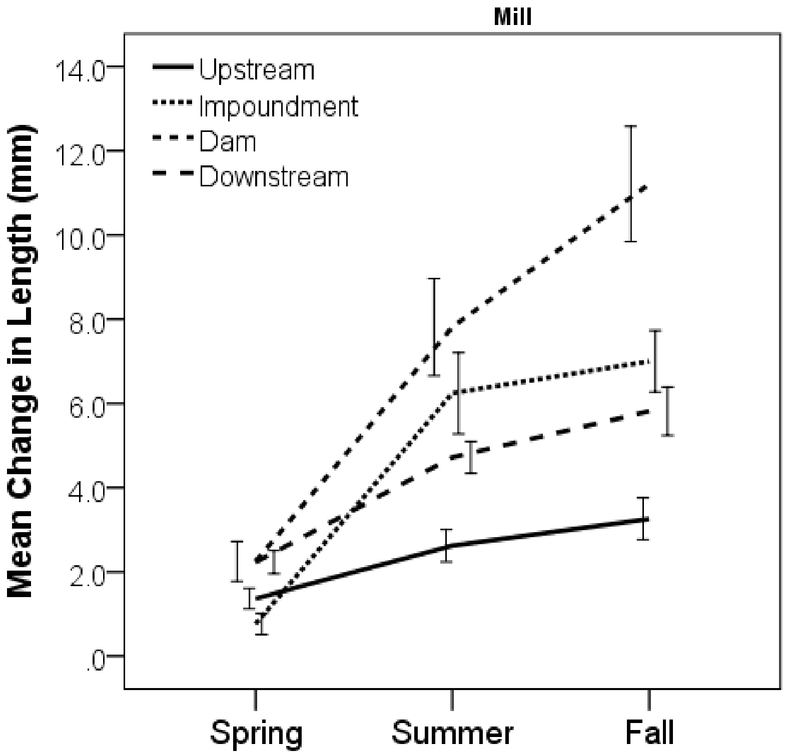

Figure 2. Seasonal mean change in mussel length (mm) within mill reaches. Solid line represents upstream reach, dotted line represents impoundment reach, short dashed line represents dam reach and long dashed lines represent downstream reach. Bars represent ± 2 SE.

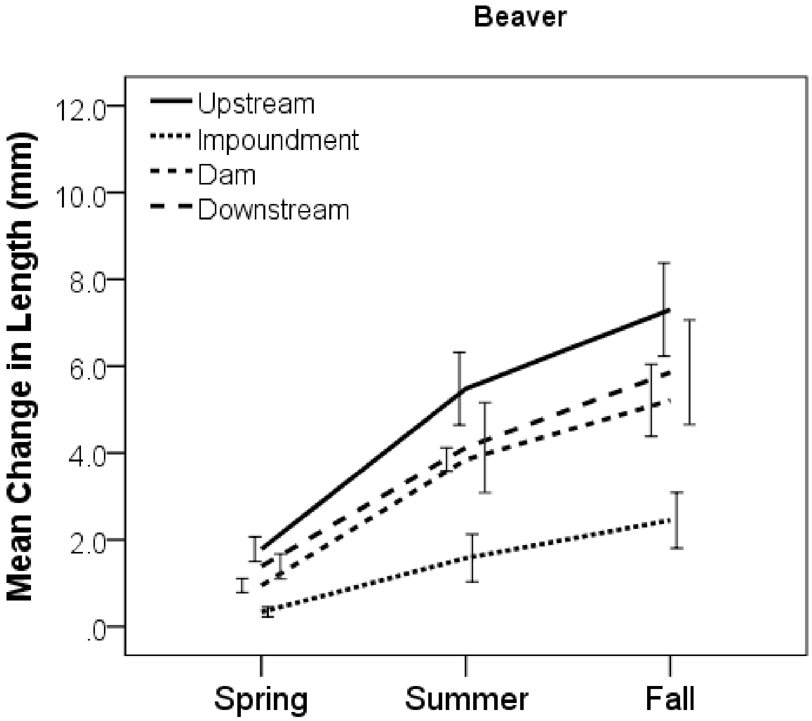

Figure 3. Seasonal mean change in mussel length (mm) within beaver reaches. Solid line represents upstream reach, dotted line represents impoundment reach, short dashed line represents dam reach and long dashed lines represent downstream reach. Bars represent ± 2 SE.

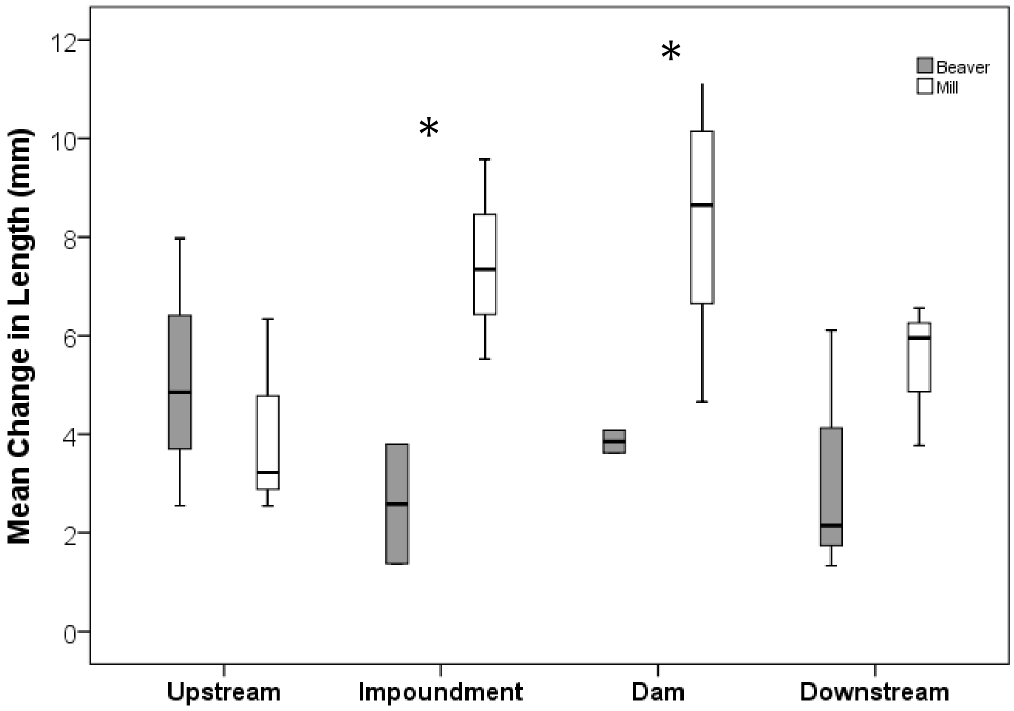

Figure 4. Reach scale mean change in mussel length (mm) between treatments and among reaches. Dark boxes represent beaver reaches and white boxes represent mill reaches. Bars represent ± 2 SE. * Represent significant differences between treatments, $P < 0.05$.

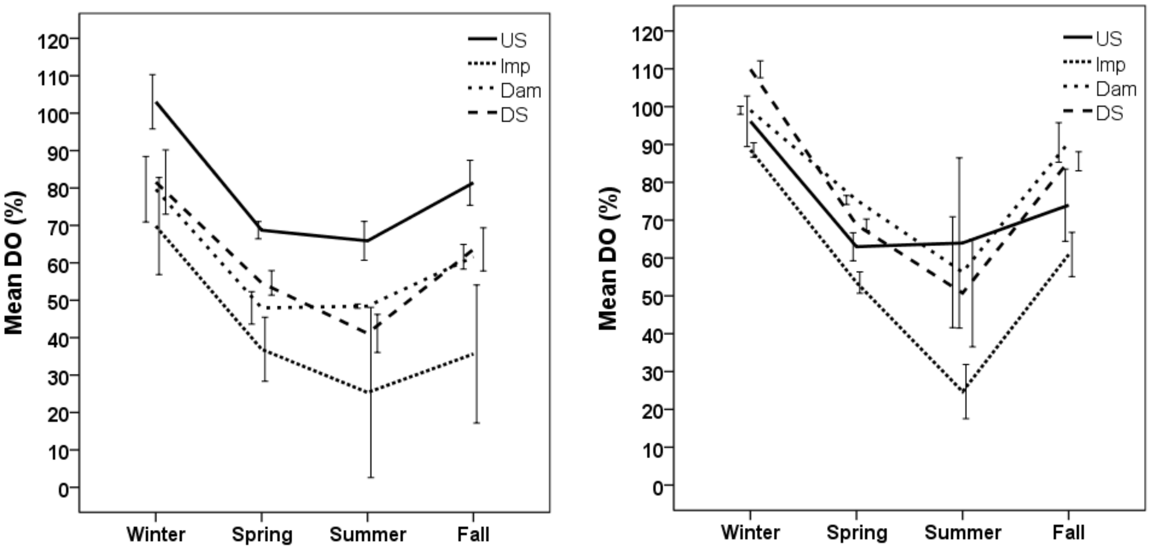

Figure 5. Mean dissolved oxygen (%) in beaver reaches and mill reaches. (A) Represents beaver reaches and (B) represents mill reaches. Solid line represents upstream reach, dotted line represents impoundment reach, short dashed line represents dam reach and long dashed lines represent downstream reach. Bars represent ± 1 SE.

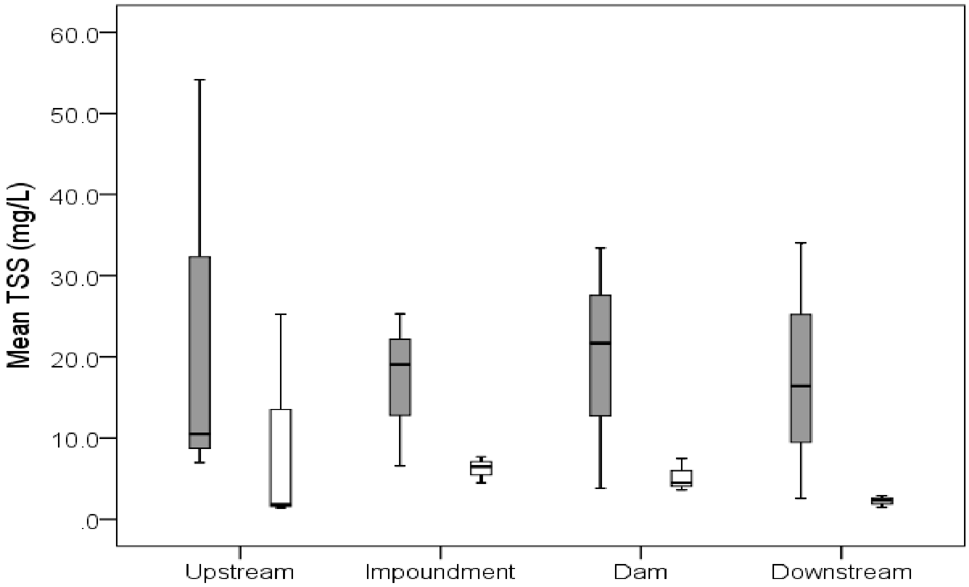

Figure 6. Mean TSS (mg/L) between treatments and among reaches. Dark boxes represent beaver reaches and white boxes represent mill reaches. Bars represent ± 2 SE.

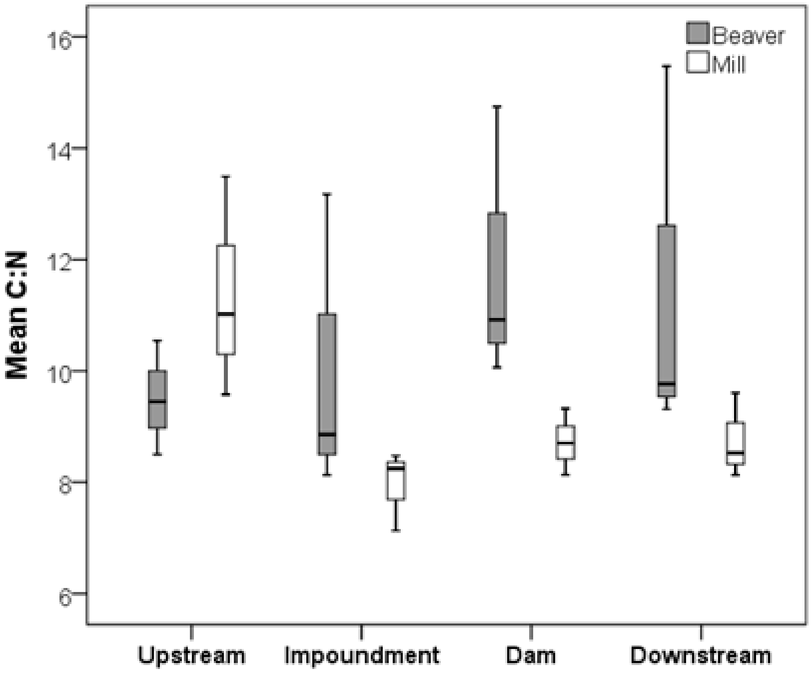

Figure 7. Mean carbon:nitrogen ratios between treatments and among reaches. Dark boxes represent beaver reaches and white boxes represent mill reaches. Bars represent ± 2 SE. * Represent significant differences between treatments, $P < 0.05$

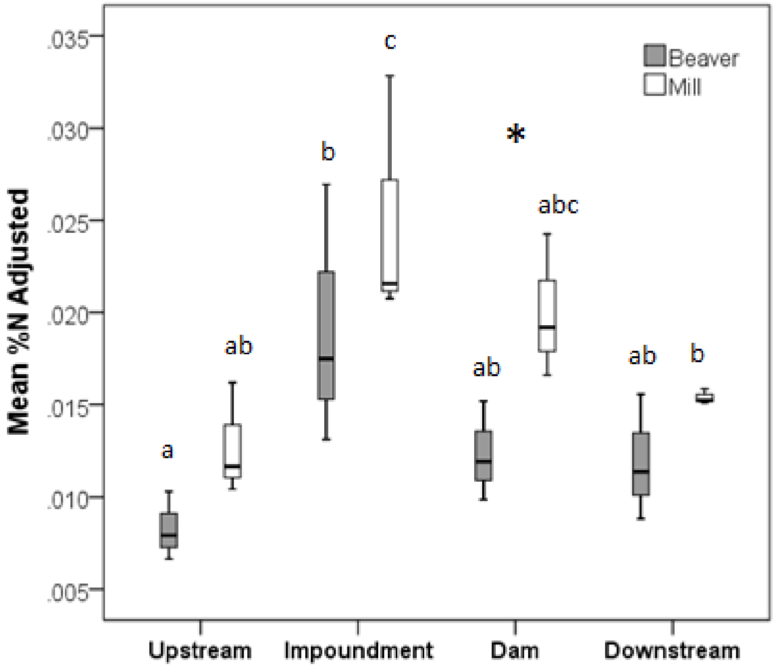

Figure 8. Mean % nitrogen (adjusted) between treatments and among reaches. Dark boxes represent beaver reaches and white boxes represent mill reaches. Bars represent ± 2 SE. * Represent significant differences between treatments. Different letters represent significant differences between reaches within the same treatment, $P < 0.05$

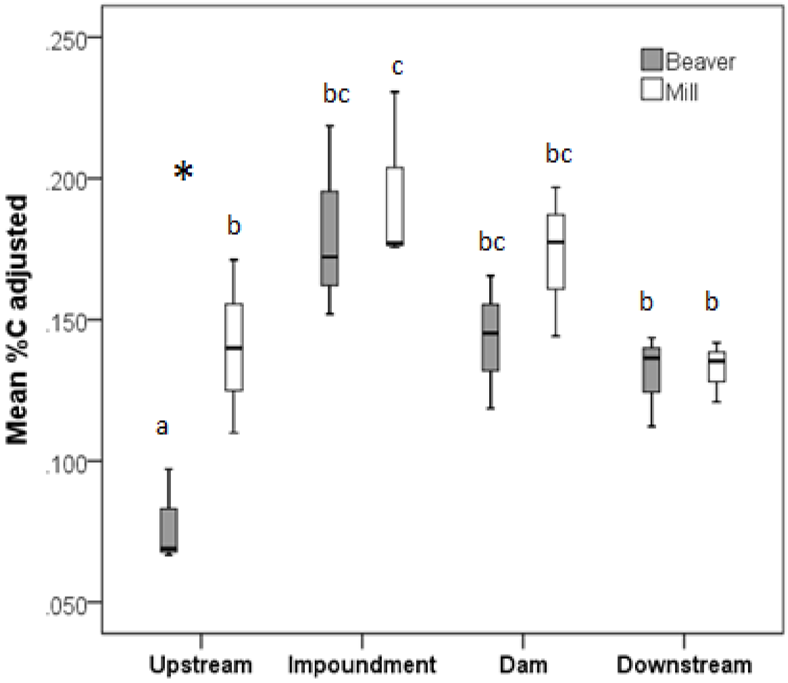

Figure 9. Mean % carbon (adjusted) between treatments and among reaches. Dark boxes represent beaver reaches and white boxes represent mill reaches. Bars represent ± 2 SE. * Represent significant differences between treatments, $P < 0.05$. Different letters represent significant differences between reaches within the same treatment, $P < 0.05$.

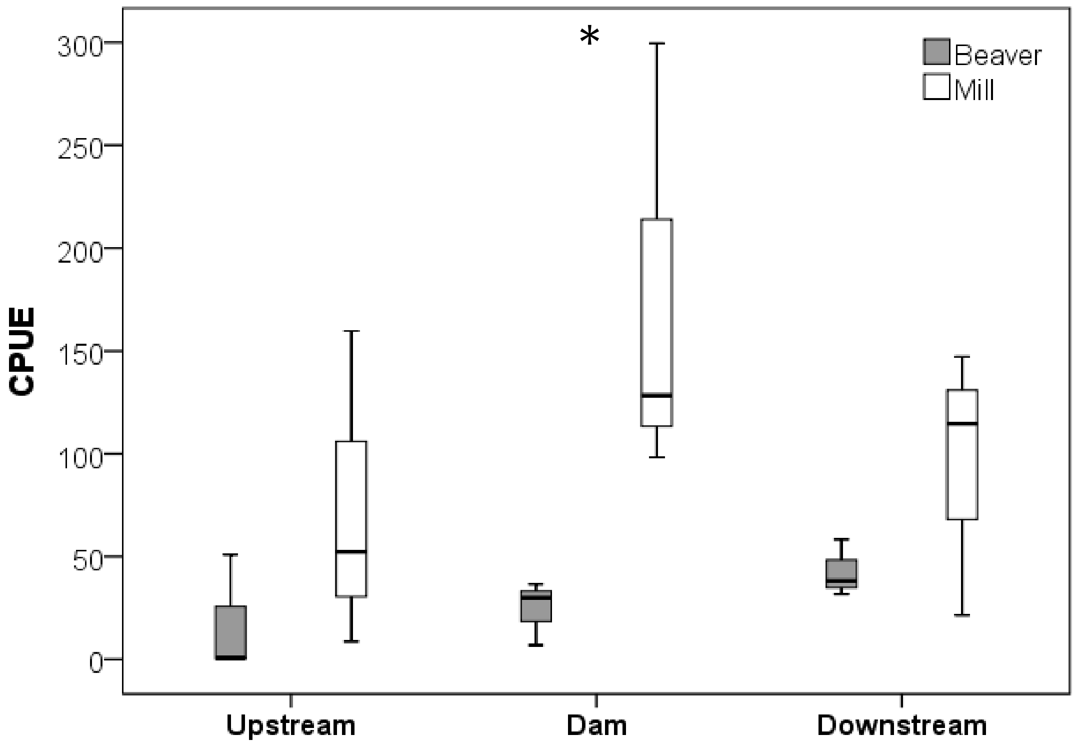

Figure 10. Mean CPUE between treatments and among reaches. Dark boxes represent beaver reaches and white boxes represent mill reaches. Bars represent ± 2 SE. * Represent significant differences between treatments, $P < 0.05$.

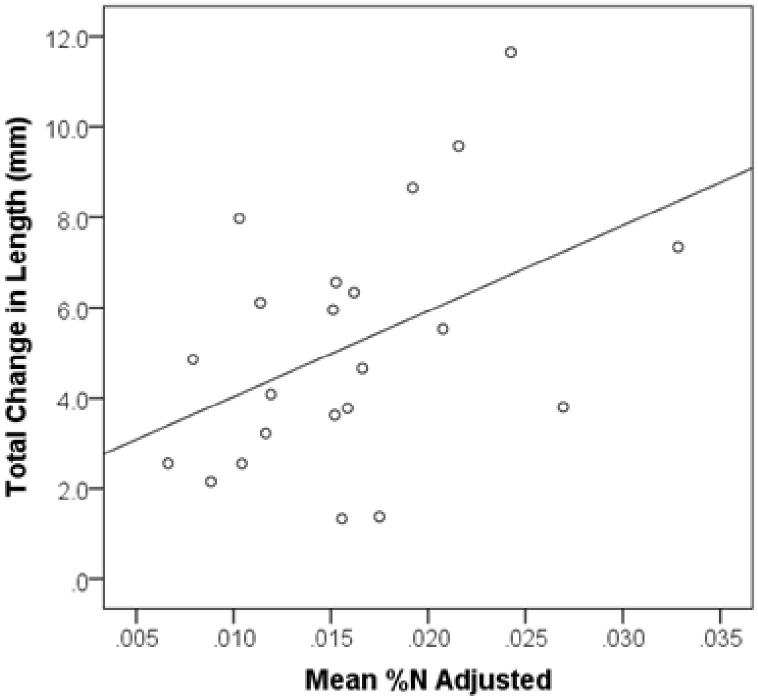

Figure 11. Relationship between % nitrogen (adjusted) and change in mussel length (mm).

VITA

Ms. Rachael Ann Hoch was born in Raleigh, North Carolina on January 27, 1986 to Thomas and Darla Hoch. She attended elementary through high school in Fuquay-Varina and graduated from Fuquay-Varina High School in 2004. In the fall of 2004, she entered Appalachian State University to pursue a degree in biology with a focus on environmental science and conservation biology. In May of 2008, she was awarded her Bachelor of Science degree. In the spring of 2010, she accepted an assistantship at Appalachian State University to pursue a Master of Science degree. In December of 2012, she was awarded the MS in biology.

During her undergraduate tenure at Appalachian State University, she worked on a variety of renewable energy initiatives and served as the President of the Appalachian State University Renewable Energy Society. During her Master's tenure, she worked at the North Carolina Wildlife Resources Commission's Marion Conservation Aquaculture Center focusing on the propagation and conservation of endangered freshwater mussels and fishes.