

**EFFECTS OF SMALL DAMS ON FRESHWATER BIVALVE ASSEMBLAGES
IN NORTH CAROLINA PIEDMONT AND COASTAL PLAIN STREAMS**

A Thesis
by
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ABSTRACT

EFFECTS OF SMALL DAMS ON FRESHWATER BIVALVE ASSEMBLAGES IN NORTH CAROLINA PIEDMONT AND COASTAL PLAIN STREAMS (May 2012)

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Small dams represent one of the most widespread human alterations to North American streams, yet their effects on imperiled native freshwater bivalve assemblages are greatly understudied. Small dams are being removed at an accelerating rate and prioritizing dams for removal presents a challenge for resource managers also tasked with preserving imperiled taxa. My study examined the effects of dam condition (8 intact, 8 breached, 7 relict) on bivalve assemblages in three North Carolina river drainages (Tar, Neuse and Roanoke) from 2009-2011. I qualitatively and quantitatively sampled bivalve assemblages within three 150-m reaches associated with each dam. I found that streams with small intact dams support more mussels, higher richness, and greater numbers of imperiled species compared to streams with breached or relict dams. Mill reaches of intact dams had higher mussel abundance (as both density and CPUE) compared to up- and downstream reaches. Interestingly, mill reaches of intact dams had larger *Elliptio complanta* (the most abundant taxon across all sites) compared to up- and downstream reaches, suggesting that mussels in the mill reach exhibit more rapid growth and reach larger sizes relative to conspecifics in other reaches. Small dams may stabilize or moderate upstream landuse effects and provide mussels with enhanced food resources. My data suggest that un-controlled dam removals may have profound negative consequences for mussels and future restoration projects need to

assess trade-offs between ecological and species-specific costs and benefits of decisions regarding imperiled aquatic biota.

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INTRODUCTION

Human-constructed dams have existed for centuries on the world's waterways. Dams have been constructed for many purposes, including hydroelectric power, navigation, flood control, drinking water reservoirs and recreation (Petts 1984; Graf 1999). In North America, only 42 rivers >200 km are believed to remain free-flowing in the 48 contiguous states (Benke 1990). There are >2 million dams in the United States, including 84,000+ high enough (>2 m height) to be listed as dams by the U.S. Army Corps of Engineers and the National Inventory of Dams with their criteria (NID, <http://nid.usace.army.mil>). NID reports the greatest density of dams occurs in southeastern states with North Carolina reporting 3,382 dams and 1,796 (35%) of those are < 7 m in height.

Dams physically modify free-flowing rivers into lacustrine environments and dramatically alter community structure and ecological function (Poff & Hart 2002). Dam effects can extend for considerable distances up- and downstream and hydro-peaking operations may alter stream discharge and physicochemical parameters including DO, temperature, conductivity and pH (Baxter 1977; Ward & Stanford 1979). Reservoirs concentrate nutrients and other pollutants, increase retention of fluvially-transported materials and dramatically alter water quality within reservoirs and tailwaters (i.e., the reach immediately downstream from a dam, Hannan 1979; Petts 1984). In addition, dams disrupt fluvial sediment migration patterns, increase upstream siltation (within impounded area) and downstream channel scouring. Dams may also fragment populations and reduce gene flow and ultimately, genetic diversity of isolated populations (Watters 1996; Jansson et al. 2000;

Neraas & Spruell 2001; Tiemann et al. 2004; Yamamoto et al. 2004).

Small dams associated with water-powered mills (e.g., grist-mills) were common in the southeast throughout the 18th and early 19th centuries (Graf 2005). Walter and Merritts (2008) estimate that >65,000 water-powered mills existed in the eastern United States by 1840. Currently, intact, breached and relict low-head dams are widespread in southeastern streams and impound small to-moderate length reaches. Very large dams (e.g., hydroelectric power dams >10 m) were not built until the 20th century and as development for river resources attracted more government and private interests, the mid-20th century became an era of extensive dam construction in North America (Graf 2005). Approximately a quarter of the presently existing U.S. dams were built prior to 1960 (<http://nid.usace.army.mil>) but frequently their ecological effects were not apparent until decades later.

Freshwater mussels

Freshwater mussels (Bivalvia: Unioniformes: Unionidae and Margaritiferidae) play important roles in stream ecosystems including removal of suspended material from the water column, increasing water clarity, serving as links in nutrient cycling and even altering physical habitats (Vaughn et al. 2008; Williams et al. 2008). North America supports the most diverse freshwater mussel assemblage in the world with 300+ species including numerous drainage and regional endemics (Neves et al. 1997). Freshwater mussels, like many other southeastern riverine taxa are highly imperiled; some estimates place 50-75% of North American mussel taxa at risk of extinction (Williams et al. 1993; Ricciardi & Rasmussen 1999; Watters 2001; Wilcove & Master 2005; Bogan 2008; Williams et al. 2008). North Carolina historically supported 49 freshwater mussel species but has experienced

among the most dramatic mussel declines in the region with 59% (29 spp.) of all native unionids extirpated or at risk of becoming extinct (Neves et al. 1997; Bogan 2007; Haag 2010).

Mussels require clean, flowing water, stable substrates, sufficient food and moderate to high concentrations of dissolved ions in order to survive (Strayer & Ralley 1993; Vaughn 1997). Mussel population declines and range contractions are believed attributable to a variety of factors including landuse-mediated changes to nutrient or sediment regimes, toxicants, invasive species, dredging, channelization, and habitat loss associated with dams (Lydeard et al. 2004; Strayer et al. 2004).

Invasive species

Native mussels are likely affected by the invasive Asiatic clam, *Corbicula fluminea* (Clarke 1988; Strayer 1999). *Corbicula fluminea* were first reported in the western United States in the early 1900's and since then have spread rapidly throughout North America (Counts 1986). Because *C. fluminea* is also a burrowing, filter-feeding bivalve and may occur in dense aggregations (Hakenkamp et al. 2001) it is a likely competitor with unionids, but empirical evidence for competitive exclusion is lacking. Although *C. fluminea* is morphologically and ecologically similar to unionids, they differ in some basic life-history characteristics. For example, native mussels are typically large (>300 mm length), slow-growing, long-lived (some taxa >100 years old) and may not reach maturity until 6–12 y (Vaughn & Spooner 2006). Mussels are also obligate fish parasites and this unique strategy presumably facilitates dispersal (Kat 1984; McMahon & Bogan 2001). In contrast, *C. fluminea* are small (<50 mm), live 1–5 y, grow rapidly, mature quickly and when mature may

often reproduce multiple times per year (McMahon & Bogan 2001). These life history traits as well as its popularity as bait have contributed to its success and *C. fluminea* has colonized nearly every permanent waterbody in the southeastern United States.

Despite their ubiquity, few studies have quantified associations between *C. fluminea* and native mussels. This may be due in large part to a lack of quantitative baseline (pre-invasion) data and also with difficulties in comparing results of studies conducted across multiple spatial scales and/or sampling efforts (Strayer 1999; Vaughn & Spooner 2006). Some studies have reported that *Corbicula* and native mussels have non-overlapping distributions, suggesting *Corbicula* out-compete unionids or are abundant where mussels are rare and vice versa (Kraemer 1979; Clarke 1986, 1988). Strayer (1999) proposed that *Corbicula* may invade sites where mussel populations are already in decline or they may simply live in different micro-habitats than mussels. However, there are also examples of *Corbicula* and mussels co-existing in dense aggregations (Clarke 1988; Miller & Payne 1994). More quantitative data are needed to fully understand relationships between invasive and native mollusks.

Habitat and freshwater mussels

Strayer (2008) identified 5 factors; dispersal, habitat, fish hosts, food and predation that may affect freshwater mussel distributions. Understanding how mussels respond to these factors is an increasingly important component of mussel conservation (Vaughn 1997). The River Continuum Concept (RCC) proposed by Vannote et al. (1980), is a conceptual framework that views streams as longitudinally linked systems where downstream communities and ecosystem function are dependent upon upstream ecosystem processes and

changing stream morphology. The RCC provides a model for predicting biological interactions of lotic systems with the geomorphic environment. It also provides a framework for understanding and interpreting how lateral changes in stream community structure and function respond to changes in geomorphic, physical, and biotic variables associated with impacts, including dams.

Regional and localized land use may play a critical role in shaping mussel assemblages (Brim-Box & Mossa 1999; McRae et al. 2004). Land use can influence discharge, water velocity, temperature and sediment dynamics (e.g., deforested or impervious land has poor water retention, increased sediment run-off and higher summer water temperatures due to less canopy cover), all factors likely to affect mussels (Morris & Corkum 1996; Brim-Box & Mossa 1999). North Carolina's human population has increased dramatically over the past 20 y and is expected to continue (www.ncatlasrevisted.org). The transformation of agricultural and forested land to ex-urban developments has had a dramatic effect on streams in North Carolina's Piedmont Physiographic Province (Powell et al. 2003). This region includes seven mid-to-large sized cities (Raleigh, Durham, Chapel Hill, Greensboro, Asheboro, Winston-Salem and Charlotte). Since the early 1980's, North Carolina's loss of farmland is among the largest in the nation while the amount of urban land continues to increase significantly (Powell et al. 2003).

Dams and mollusks

North American streams have been subject to biologically-mediated impoundment for millennia. Prior to European settlement, beaver (*Castor canadensis*) were abundant in North America and populations may have been as large as ~60-400 million (Naiman et al. 1988).

Beaver alter stream geomorphology and impact stream valleys through dam construction. Beaver dams help create the wetland-dominated, multiple anabranching channels that likely characterized mid-Atlantic streams during pre-settlement times (Naiman et al. 1988; Walter & Merritts 2008). In the early 17th century extensive beaver removal began in North America and by 1900 beaver was almost extinct (Jenkins & Busher 1979). Their absence transformed the forested wetlands, with small, shallow, interconnected pools into deeply incised streams with steep eroding banks typical of most current mid-Atlantic Piedmont streams (Walter & Merritts 2008). Thus, historical and current land use may provide further insight into the mussel assemblage patterns observed in my study in east-central North Carolina.

Previous studies have found that mussel populations are often strongly reduced for a considerable distance downstream from large dams and large hydro-peaking or hypolimnetic-release dams have few mussels in their tailwaters (Baxter 1977; Watters 1996; Parmalee & Bogan 1998; Vaughn & Taylor 1999; Lessard & Hayes 2003; Graf 2006; Williams et al. 2008). Mussels are sensitive to the effects of dams during all life stages. Freshwater mussels have a unique life cycle that involves an obligate parasitic larval stage, called the glochidium. Larvae attach to gills and/or fins of fish and juveniles excyst and become sedentary adults in the streambed. Parasitism presumably facilitates unionid dispersal within and between stream drainages (Watters 1992; Vaughn & Taylor 2000). Watters (1996) attributed extirpation of two mussel species upstream from dams in five North American Midwest river systems to the disappearance of fish hosts. Conversely, Smith (1985) reported that range expansion of *Anodonta implicata* was linked to the re-introduction of host fish (Clupeidae) above successive dams in the Connecticut River.

Although small dams represent one of the most widespread human alterations to North American streams, they are understudied (Graf et al. 2002; Poff & Hart 2002). Dean et al. (2002) reported significant differences in mean mussel species richness at sites associated with 2 dams on the Neosho River, Kansas. Upstream, impounded and tailwater reaches had significantly fewer species compared to both up- and downstream reference sites. Moreover, Tiemann et al. (2007) reported that low-head dams impair upstream freshwater mussel populations in the Fox River, Illinois, by creating unsuitable habitat (reservoirs) and restricting host fish distributions.

In contrast, more recent research suggests that some intact older mill dams promote or retain large, diverse and fast-growing mussel populations in downstream reaches (Gangloff et al. 2009a; Gangloff et al. 2011; Singer & Gangloff 2011). Removal of dams may trigger release of entrained substrates and geomorphic adjustments that may be detrimental to downstream mussel populations (Stanley & Doyle 2002; Stanley et al. 2002; Doyle et al. 2003; Sethi et al. 2004). Gangloff et al. (2011) reported that Alabama streams with breached dams had relatively few mussels and retained a low proportion of historical assemblages suggesting that un-controlled dam removals may have profound negative consequences for downstream mussels.

Small dams are being removed at an accelerating rate due to maintenance and liability concerns as well as for ecological benefits (Poff & Hart 2002). Prioritizing dams for removal presents a challenge to resource managers tasked with preserving and enhancing imperiled freshwater mollusks and their habitats. Dam removal projects are increasingly common components of stream restoration projects and present an opportunity for scientists to study the effects of restoration on biota and habitats. My study examines whether freshwater

bivalve assemblages in North Carolina streams are different in the vicinity of intact, breached and relict dams. I examined small dam effects on small to mid-sized streams in three North Carolina drainages with endemic but highly-imperiled mussel assemblages. Specifically, my study addresses the following questions: 1) How are bivalve assemblages in streams associated with dams affected by dam condition? (i.e., are there differences in bivalve density, mussel catch-per-unit-effort, richness, size and abundance of rare species)? 2) Do drainages and streams explain any variation in bivalve responses to dam condition? 3) How do dam-mediated/landscape factors affect bivalve assemblages? (i.e., land use, physical habitat, host fish, and invasive *Corbicula fluminea*).

METHODS

Study sites

My study examined effects of dam condition on bivalve assemblages in small to mid-sized (i.e., 2nd-6th order) east-central North Carolina streams. I established 69 study sites associated with 23 dams in three different conditions (8 intact, 8 breached and 7 relict dams) in the Neuse, Roanoke and Tar River drainages. These drainages support moderately diverse Atlantic Slope mussel assemblages (Neuse and Tar = 24 taxa, Roanoke = 22 taxa, Bogan 2007). Intact dams form a nearly complete channel barrier and impound upstream reaches under most flow conditions. Breached dams partially (25-95%) obstruct the channel and may impound a short-to-substantial (>2 km in my study streams) upstream reach depending on dam size. Relict sites were either actively removed (e.g., Cherry Hospital and Lowell Mill dams on the Little River) or failed during flood events and often exhibit little evidence that a dam was present.

Dams were located primarily in the Piedmont Physiographic Province of North Carolina ($n = 15$) but several ($n = 8$) were located in the Coastal Plain (Fig. 1, Table 1). East of the Blue Ridge Mountains, the Piedmont Plateau surface slopes for ~200 km in North Carolina to an elevation of 120 or 150 m at the fall line marking the transition to the Coastal Plain Physiographic Province (Oosting 1942). Piedmont streams have moderate to high gradient and velocity waters including numerous shoals, rapids and bedrock outcroppings alternating with calm stretches of low to moderate velocities and relatively coarse substrates. In contrast, coastal plain streams have much lower gradient channels and a more

heterogeneous mixture of substrates.

Several target streams were designated as sensitive waters (i.e., streams supporting federally-listed fish or mussels) by the North Carolina Wildlife Resources Commission (NCWRC). Sensitive waters include Little River and Contentnea Creek (Neuse Drainage), the upper Dan and Mayo rivers (Roanoke Drainage), the upper Tar River and tributaries including Fishing and Sandy creeks (Tar Drainage). Dam localities were acquired from the Geographic Names Information System (GNIS) database (www.geonames.usgs.gov), the North Carolina Department of Environment and Natural Resources dam database (www.dlr.enr.state.nc.us), and from the North Carolina Atlas & Gazetteer (Delorme Map 2003). Sites were also selected after consultation with NCWRC personnel.

Bivalve surveys

I sampled bivalve assemblages within three 150-m reaches for each dam site. The upstream reach was >500 m upstream from the impoundment (or the formerly impounded zone), the mill reach was immediately downstream (0-150 m) of the dam, and the downstream reach was located ≥ 500 m (typically 500-650 m) downstream from the dam. Cross-channel transects were established at 10-m intervals within the 150-m study reach ($n = 15$ per reach, $n = 45$ per site). In order to accurately characterize mussel abundance and assemblage composition, I conducted both quantitative and qualitative mussel surveys (Miller & Payne 1993; Obermeyer 1997; Vaughn et al. 1997; Gangloff et al. 2011). To quantify mussel density and demography I excavated (to a depth of ~10 cm) and sieved (through 6 mm mesh) five evenly-spaced 0.25-m² quadrats along each transect ($n = 75$ per reach, $n = 225$ per site). Non-unionid bivalves (Sphaeriidae and *Corbicula fluminea*) were

also enumerated.

In order to detect rare mussels I also used intensive, timed visual-tactile searches to sample the 10-m sections between transects ($n = 15$ searches per reach, $n = 45$ per site). All mollusks were identified in the field to the lowest practical taxonomic level following Bogan (2007), enumerated, measured (total length) and returned to their approximate point of capture. When possible, unionids were sexed, aged and reproductive condition noted. Mollusks not readily identifiable in the field (e.g., some *Elliptio* and Sphaeriidae) were preserved in alcohol and returned to the laboratory for identification and possible subsequent genetic analyses. All shell and whole specimen vouchers will be deposited in the North Carolina Museum of Natural History in Raleigh, NC.

Mussel length and dams

Previous research suggests that mussels living immediately downstream from small intact dams are larger and grow faster than mussels located up-or-downstream and is likely due to impoundment-enhanced food quality and quantity (Singer & Gangloff 2011). To examine the ubiquity of this pattern I measured the length of all *Elliptio complanata* found during quadrat excavations ($n = 1,656$) and plotted reach-scale length-frequencies for each dam type. I did not use data from time-searches because they are likely biased towards larger animals. I used 1-way analysis of variance (ANOVA) to assess differences in *E. complanata* length among dam types (intact, breached and relict) and Tukey HSD post-hoc tests to examine differences between reaches of dam types.

Mussel host fish collection

I collaborated with Holcomb et al. (unpublished), who conducted fish surveys at all study sites in 2010-2011, to address the hypothesis that mussel aggregations below intact mill dams is caused by host fish distributions. Fish were sampled from 12 replicate meso-habitats per reach (3 each of bank, riffle, run and pool). Sampling was conducted for 100 seconds per replicate meso-habitat with a Smith-Root LB-12 backpack electro-fisher and seines. Seines were used to sample deeper (>1.5 m) pools. If a new species was obtained on the last replicate of a given meso-habitat, a new meso-habitat of the same type was sampled for an additional 50 seconds. Additional replicates were sampled until no new species were detected. All fish were identified to species, measured (standard length) and weighed (if >10 g) and returned to the stream. Mussel host designations were obtained from Ohio State University's Division of Mollusks database (www.biosci.ohio-state.edu/~molluscs/OSUM2) and mussel propagation director Chris Eads from North Carolina State University.

I calculated four different site-scale mussel host-fish metrics to test the hypothesis that mussel assemblages near dams are correlated to host-fish distribution. The total number and percentage of fishes and fish taxa that were sampled that are known to be mussel hosts were computed for every site. All host-fish data were normally distributed (Shapiro-Wilk $p > 0.05$) except the number of mussel host-fish, which was log transformed prior to analyses. I used 1-way ANOVAs to test for differences in mussel host-fish metrics across dam types and I used Tukey HSD post-hoc tests to examine differences in fish host assemblage metrics between reaches.

Habitat measurements

To assess the impact of small dams on physical habitats, I measured habitat parameters at fine and broad spatial scales (i.e., quadrat, transect, site and catchment scale). I measured water depth, the distance to nearest bank, current velocity, and substrate composition for all quadrats. I measured water depth (m) and current velocity (mid-channel velocity, m/s) in the center of each quadrat with an electronic flow meter (Marsh-McBirney Flo-Mate, model 2000) and measured (largest diameter, mm) or categorized 12 substrate particles per quadrat ($n = 60$ per transect) using a modified Wolman pebble count (Wolman 1954). Un-measurable substrates were characterized as bedrock, mudstone, clay, silt, or sand and non-lithic particles were categorized as organic matter (leaves, macrophytes, detritus), or wood. All habitat variables were measured under summer or fall baseflow conditions, typically during or immediately following mussel surveys.

I calculated both the mean and median particle diameter and the proportion of the streambed that was comprised of particles and unmeasured particles (e.g., bedrock, wood, organic matter, mudstone, clay, sand and silt). To assess if broad-scale habitat characteristics vary across dam types, I pooled reaches together within each dam type and calculated site-scale means for all streambed physical habitat parameters. I used Spearman correlations to examine associations between site-scale bivalve assemblage metrics and stream habitat parameters.

I also measured stream chemical parameters at all reaches. I measured DO, % O₂ saturation, temperature, conductivity, specific conductance, and pH using a YSI model 55 DO meter and a YSI model 63 conductivity-pH meter. I continuously monitored water temperature (every 4 hours) with NexSens micro-T Temperature data loggers at all reaches.

Data loggers were retrieved bi-annually from summer/fall 2010 to 2011 to calculate mean monthly temperatures. Daily water temperature means were calculated for dams which had loggers retrieved from all reaches ($n = 13$), however only a few of those dams had complete 2010-2011 data to compare between reaches for analysis.

I analyzed temperature data for each dam separately and used ANCOVA to model effect of reach position (up- and downstream of dams) and time (month) on water temperatures. I modeled reach as the independent variable, temperature as the dependent variable and month as the covariate. Due to significant interactions between reach and month, I compared monthly reach-scale mean temperature data at each dam using 1-way ANOVA to test the hypothesis that temperature differed among reaches. Tukey HSD post-hoc tests were used to examine pairwise differences between reaches.

Landuse parameters

I collaborated with Gabriel Upchurch (University of Tennessee Knoxville) and used ArcGIS (Version 10.0, ESRI, Redlands, CA) to obtain landscape-scale habitat and landuse classification data including upstream catchment area (km^2), rank and link magnitude (the number of upstream first order tributaries) and percentage of surface cover comprised of 13 land use classes (open water, wetland, high-intensity urban, low-intensity urban, total urban intensity, pasture, row-crop agriculture, deciduous, evergreen, mixed and total forest, grassland, and barren ground). I delimited watersheds and calculated land use attributes for 57 sites associated with 12 Piedmont and 8 Coastal Plain dams. Worsham, Long and Chandler Mill dams were excluded as were the downstream reaches of 2 Coastal Plain dams and 1 Piedmont dam due to insufficient land use data collection. I excluded land use

categories from analyses if the mean percentage of surface cover was ≤ 1 (e.g., at all 57 sites open water mean = 0.87% and barren land mean = 0.17%). However, I computed total urban intensity (low + high) for analyses due to percentage of urban high surface cover being < 1 . Total forest = the sum of deciduous, evergreen and mixed forest. I used Spearman correlations to examine associations between site-scale bivalve assemblage metrics and landuse parameters.

High conservation concern mussels

I obtained mussel Global (GHR) and State (SHR) Heritage rankings from NatureServe Explorer (www.natureserve.org/explorer). NatureServe assigns both a global and state conservation status rank to all species tracked on its Explorer online database. A species' global heritage rank (GHR) is a range-wide assessment of condition. State conservation status varies broadly, and state heritage ranks (SHRs) are a more conservative assessment of a species' local or regional condition. Species with a GHR/SHR = 1 are most imperiled and those with a GHR/SHR = 5 are least imperiled. I computed both reach and dam-scale (i.e., all three reaches associated with dam site) mean GHR and SHR for mussel assemblages.

Statistical analyses

I used SPSS software (Version 19.0, SPSS, Chicago, IL) for all statistical procedures. Two dams on streams with no mussels, Chandler Mill and Worsham Mill, were removed prior to analyses because it is difficult to infer dam effects in streams with no mussels. All biotic data were transformed ($\sqrt{[n+1]}$), unless stated otherwise, to improve normality.

Because scale has fundamental significance and the patterns that are unique to any range of scales for a given species will have unique causes and biological consequences, I compiled bivalve data at both transect- and reach scales prior to analyses (Levin 1992). Bivalve abundance was computed as density (number individuals/m²) from quadrat samples. Mussel abundance was computed as catch-per-unit-effort (CPUE) from timed-search samples. Mussel diversity was quantified by calculating both Shannon-Wiener (H') and Simpson (D) indices at the reach scale. Shannon H' is a function of species proportions in a sample and takes into account the number of species and the evenness of the species present (Shannon & Weaver 1949). Simpson's Index (1-D) is a measure of the concentration of species and is sensitive to the abundance of more plentiful species in a sample (Simpson 1949).

Site-scale analyses

I used general linear models (GLMs) to examine the effects of dam status (intact, breached, relict), stream drainage (Neuse, Roanoke, Tar) and reach position (upstream, downstream, mill reach) on bivalve assemblages at the site-scale. Because I found significant drainage effects in fixed-effects models, I employed mixed-models to account for random effects associated with individual streams (e.g., land use history, local geology) within drainages and to assess the impact of stream identity on bivalve responses to dam status. However, including the random factor (stream nested within drainage) in my models did not further explain variance among my data at the site-scale ($z > 0.05$, $p > 0.05$ for all bivalve assemblage metrics). Therefore I proceeded with a GLM approach and assessed within-stream patterns of dam condition on bivalve assemblages in separate drainages.

Since my study utilizes a 'natural' experimental design (i.e., treatment = existing dam

condition), I used log response ratios to quantify proportional changes to bivalve assemblage parameters up- and downstream from dams with GLM ANOVAs (Hedges et al. 1999).

Response ratios (RR) are often used as standardized measures of effect magnitude in ecology and I employ them to standardize dam effects across different stream types and sizes (Schmitz et al. 2000; Hebblewhite et. al 2005).

I calculated RRs using untransformed reach-scale means of bivalve assemblage metric data. I calculated the response ratios X_e/X_{cu} and X_e/X_{cd} where X_e is the response variable (abundance, diversity) in the experimental treatment (i.e., mill reach) and X_{cu} and X_{cd} is the same variable in the upstream (X_{cu}) and downstream (X_{cd}) control reaches and then RR were log transformed. A positive RR (e.g., mussel density mill/downstream RR) infers a positive effect of the dam (i.e., higher mussel density in the mill reach than downstream) on bivalve assemblage parameters and a negative RR infers a negative effect (i.e., lower mussel density in the mill reach than downstream). Within drainages, I modeled effects of dam status on bivalve RRs which allowed me to directly assess stream-specific effects of reach position (i.e., up- or downstream of dams).

Transect-scale analyses

Due to significant drainage effects in GLMs in site-scale analyses, I assessed bivalve responses to dam condition at the transect-scale ($n = 1,034$) with mixed-models to account for random effects associated with individual streams within drainages. There were significant interactions between reach and status so I analyzed effects of reach on bivalve parameters within each dam status separately while controlling for random effects associated with streams.

RESULTS

Bivalve assemblages

I collected and identified 54,249 mussels (19 taxa) during timed-searches and obtained measurements on 2,250 mussels (from 17 taxa) collected during quadrat sampling (Tables 2-4). Additionally, 81,184 *Corbicula fluminea* were collected. Study streams supported a moderately diverse mussel assemblage that was dominated by *Elliptio complanata* (79% of individuals from timed-searches) and 86% of individuals were members of the *E. complanata* complex (e.g., *E. congaraea*, *E. mediocris*, Bogan 2007). However, I also detected populations of 10 state-or-federally-listed mussels in study reaches (Tables 2-4).

Mussel abundance ranged from 0 to 9,827 individuals per site ($\bar{x} = 786$ per site) and CPUE ranged from 0 to 682 individuals per hour ($\bar{x} = 60$ /hour). Mean site-scale mussel density ranged from 0 to 15.84 mussels/m² ($\bar{x} = 2.0$ mussels/m²). Site-scale mussel richness ranged from 0-10 species (\bar{x} richness = 4 taxa/site). Because *E. complanata* dominated mussel assemblages, diversity was low (Shannon H' overall $\bar{x} = 0.28$, site-scale mean H' ranged from 0 to 0.89; Simpson D overall $\bar{x} = 0.19$, site-scale D ranged from 0 to 0.68). *Corbicula fluminea* site-scale mean density ranged from 0 to 466.8 *Corbicula*/m² (overall $\bar{x} = 72.16$ *C. fluminea*/m²).

The relationship between *C. fluminea* and mussel densities at the site-scale ($n = 54$) is significantly positive ($r_s = 0.53$, $p < 0.001$). However, the relationship produced a scatter pattern resulting in dense aggregations of points < 5 mussels/m² and transects with low

mussel density encompassed a wide range of *C. fluminea* densities. To assess the effect of dam condition on the correlation between native and invasive bivalve densities, I analyzed the relationship in streams of a given dam type separately. The relationship is not statistically significant in streams with breached dams ($r_s = 0.409$, $p = 0.065$, Fig. 2A) and is slightly significant in streams with relict dams ($r_s = 0.585$, $p = 0.046$, Fig 2B). There is a significant positive relationship between mussel and *C. fluminea* density in streams with intact dams ($r_s = 0.541$, $p = 0.011$, Fig. 2C). The scatter plot includes the same threshold at 5 mussels/m², where the range of *C. fluminea* density is greater below that threshold for each dam type (Fig. 2).

Dams and mollusks at site-scale

General linear models (GLMs) revealed strong effects of drainage on multiple mollusk assemblage metrics including the abundance, richness, and diversity of native mussels and *C. fluminea* abundance (Table 5). Including drainage and individual streams into mixed-model analyses did not improve model fit for site-scale bivalve assemblage metrics, so within-stream RR GLMs were conducted within drainages to assess dam condition on bivalve assemblage data. GLMs revealed a significant effect of dam status on *Corbicula fluminea* densities at the site-scale ($F_{2,59} = 5.677$, $p = 0.006$) and Tukey HSD post-hoc tests revealed streams with intact dams had significantly higher *C. fluminea* densities compared to streams with breached and relict dams (both $p < 0.05$, Fig. 5A, Table 7). GLMs revealed no significant RR relationships between dam types for mussel diversity or *C. fluminea* density within drainages. Further, there were no significant differences in mill/upstream RRs between dam types.

GLMs revealed that dam type had a significant effect on Tar Drainage mill/downstream total mussel abundance RR ($F_{2,8} = 6.217$, $p = 0.034$, Table 6). Tukey HSD post-hoc tests revealed that Tar Drainage intact mill/downstream (M/DS) RRs were significantly different from breached M/DS RRs ($p = 0.03$). Intact dam M/DS total mussel RRs were positive, implying a positive effect of the dam but breached RRs were negative. Tar Drainage intact dam mill reaches had significantly higher mussel abundance compared to downstream reaches. Conversely, breached dam mill reaches had significantly fewer mussels compared to downstream reaches (Table 4).

Dam type had a significant effect on Tar Drainage mussel density M/DS RRs ($F_{2,8} = 37.786$, $p < 0.001$, Table 6). Tukey HSD post-hoc tests revealed that Tar Drainage intact M/DS density RRs were significantly different from both breached ($p < 0.001$) and relict M/DS RRs ($p = 0.005$). Intact M/DS mussel density RRs were positive while breached and relict RRs were negative. These data suggest that Tar Drainage intact dam mill reaches had higher mussel density than downstream reaches. Both breached and relict dam mill reaches had lower density mussel assemblages compared to intact dams. I was unable to compute Roanoke Drainage density RRs due to low sample size.

Though not statistically significant, dam type had a marginally positive effect on Tar Drainage mussel richness M/DS RRs ($F_{2,8} = 4.898$, $p = 0.055$, Table 6). Tukey HSD post-hoc tests revealed that Tar Drainage intact M/DS RRs were significantly different from breached dams ($p = 0.047$). Intact dam M/DS mussel richness RRs were positive and breached dam RRs were negative. These data indicate that Tar Drainage intact dam mill reaches had higher mussel richness than downstream reaches, while breached dam mill reaches had lower average mussel richness than downstream reaches (Table 4).

Dam type had a significant effect on Roanoke Drainage mussel CPUE M/DS RRs ($F_{2,5} = 19.046$, $p = 0.02$, Table 6). Tukey HSD post-hoc tests revealed that Roanoke Drainage intact M/DS RRs were significantly greater than relict M/DS RRs ($p = 0.019$). Intact M/DS mussel CPUE RRs were positive while relict RRs were negative. Roanoke Drainage mussel CPUE was higher at intact dam mill reaches compared to downstream reaches but downstream CPUE was higher at relict dams.

Dams and mollusks at transect-scale

Mixed-model analyses revealed streams with intact dams in the Neuse, Roanoke, and Tar River drainages had significantly more mussels and higher richness compared to streams with breached and relict dams (Fig. 3A, B, Table 7). Further, analyses revealed strong reach effects within a given dam type on many bivalve assemblage parameters (LSD post-hoc test, $p < 0.05$, Table 8). Mill reaches in streams with intact dams had significantly higher mussel abundance (as both CPUE and density) compared to up-and-downstream reaches (Fig. 4, Table 7). Upstream reaches in streams with breached dams had significantly fewer mussels compared to up-and-downstream reaches (Fig. 4, Table 7). Mill reaches in streams with relict dams had significantly fewer mussels compared to downstream reaches (Fig. 4, Table 7). In addition, mill reaches in streams with both intact and breached dams had significantly higher *C. fluminea* densities compared to both up-and-downstream reaches (Fig. 5B, Table 7). *Corbicula fluminea* density did not differ between reaches in streams with relict dams (Fig. 5B, Table 8).

Elliptio complanata length

I measured 1,656 *E. complanata* from quadrat excavations (\bar{x} length = 72.4 mm, range = 5.4-170.3 mm). *Elliptio complanata* were more abundant overall in streams with intact dams compared to streams with breached or relict dams (intact $n = 902$, breached $n = 466$, relict $n = 288$). However, ANOVA revealed no significant differences in mean *E. complanata* length between dam types ($F_{2,49} = 0.509$, $p = 0.604$). ANOVA revealed a significant reach effect on mean *E. complanata* length in streams with intact dams ($F_{2,17} = 5.322$, $p = 0.018$, Fig. 6). Tukey HSD post-hoc tests revealed intact dam upstream control mean *E. complanata* lengths are significantly lower compared to mill reach lengths ($p = 0.014$, Fig. 6). Mean mussel size remained elevated >500 m downstream of intact dams as there were no significant differences between mill and downstream reaches (Fig. 6). *Elliptio complanata* assemblages are comprised of all age classes at intact dam mill reaches but the length-frequency distribution is slightly right-skewed (i.e., 16% of mussels > 100 mm) whereas upstream reaches were largely devoid of mussels >100 mm (Fig. 7), further indicating rapid growth below intact mill dams.

Mussel host fish

Holcomb et al. (unpublished) sampled 17, 864 fish at my study sites during 2010-2011. A large percentage of the total number of fish captured were known mussel hosts (intact $n = 4,295$, 64.6%; breached $n = 4,606$, 73.7%; relict $n = 2,678$, 57.8%). The mean percentages of fish taxa that were known mussel hosts constituted ~50% of the fish assemblages surveyed in streams within a given dam type (intact = 46.5%, breached = 49.9%, relict = 45.7%). ANOVA revealed that the percentage of host fishes was

significantly different between dam types ($F_{2,62} = 6.447$, $p = 0.003$). Tukey HSD post-hoc tests revealed that the percentage of known host fishes differed between breached and relict dams ($p = 0.002$, Fig. 8) with breached dams supporting the largest percentage of known mussel host fish and fish taxa. However, there were no significant between-reach differences in mussel host fish metrics within dam types. The percentage of known mussel host fish and mussel CPUE exhibited a significant positive relationship ($r_s = 0.26$, $p = 0.039$). No other correlations between host-fish and mussel metrics were significant.

Habitat

Streams with intact dams had a higher percentage of gravel and cobble particles, bedrock, wood and clay compared to breached or relict dams (Fig. 9A, Table 9). The percentage of sand and silt substrates was highest in streams with breached and relict dams (Fig. 9A, Table 9). However, there were few between-reach differences across dam types for most substrate categories. Mill reaches of all three dam types had higher percentages of gravel and cobble particles and lower percentages of sand and silt compared to up-and-downstream reaches (Fig. 9, Table 9).

I observed several significant relationships between mussel assemblage and stream physical habitat parameters. Mussel CPUE was negatively associated with current velocity ($r_s = -0.276$, $p = 0.029$) suggesting mussel densities may be limited by high current velocity and its effects on substrate and geomorphic parameters. Percent clay and wood were positively associated with mussel CPUE, H' and richness (Table 10). Moreover, percent sand was positively associated with mussel CPUE ($r_s = 0.266$, $p = 0.035$) and percent organic was positively associated with mussel H' ($r_s = 0.284$, $p = 0.024$). In addition, mussel H' and

richness were negatively associated with mean particle size (range = 6.5-181.3) suggesting sites with larger particles supported fewer mussels and mussel species (Table 10). I did not observe any significant relationships between *C. fluminea* densities and stream physical habitat parameters.

Temperature

Site-scale daily temperature means were analyzed between reaches within each dam ($n = 13$). There were several month-to-month differences between reaches that aided in observing thermal patterns. Across drainages, intact dam impoundments ($n = 5$) were markedly warmer (Tukey HSD, $p < 0.05$) compared to up-and-downstream reaches (e.g., Gooch's Mill, Fig. 10A). Although breached, the impoundment of Oxford City Dam was substantially warmer than up-or- downstream reaches (Fig. 10B), however other breached dams ($n = 2$) did not have impoundment loggers set for comparison. As expected, between-reach water temperatures at relict dams ($n = 6$) were not significantly different (Fig. 10C).

Landuse

On average, study sites ($n = 57$) are moderately forested (\bar{x} total forest surface cover = 54%, deciduous = 35%, evergreen = 13%, mixed = 6%, Fig. 11). Piedmont sites ($n = 35$) had more deciduous forest cover ($\bar{x} = 43\%$) than Coastal Plain sites ($n = 22$, $\bar{x} = 23.7\%$). Coastal Plain sites had more open water ($\bar{x} = 1.2\%$) and wetland surface cover ($\bar{x} = 6.1\%$) than Piedmont sites (0.7% and 2%, respectively). Spearman correlations between mussel assemblage metrics and land use revealed equivocal results, which may be due to small-scale (i.e., low percentages of surface cover) associations between factors and thus, spurious increases in the power and significance of results. I examined scatter plots to assess

relationships and identify spurious relationships that were due to high power or outliers or anomalous data points. Open water and barren land were excluded from correlation analyses (mean percentage of surface cover ≤ 1).

The proportion of wetland cover ($\bar{x} = 3.6\%$, range = 0.10 – 11.35%) was positively associated with all mussel metrics across all sites ($n = 57$, Table 11). Additionally, there was a significant positive relationship between total mussels, diversity and richness and both percent crop ($\bar{x} = 6.3\%$, range = 0.27 – 25.39%) and evergreen forest ($\bar{x} = 13.4\%$, range = 3.01 – 31.24%) surface cover. Mussel diversity and richness were negatively associated with percent deciduous forest ($\bar{x} = 35.4\%$, range = 14.79 – 61.58%) but positively associated with grassland surface cover ($\bar{x} = 6\%$, range = 1.03 – 9.59%). Mean mussel CPUE was positively associated with percent evergreen and mixed forest ($\bar{x} = 5.8\%$, range = 3.14 – 10.59%) and grassland cover. Interestingly, total urban intensity ($\bar{x} = 4.2\%$, range = 3.34 – 14.75%) was positively correlated with mussel diversity and richness.

Associations between mussel assemblage metrics and landuse at Piedmont sites were similar to those observed across all sites (Table 11). However, associations at Coastal Plain sites differed from associations at Piedmont sites and had few significant correlations, possibly due to low sample sizes (Table 11). Coastal Plain mussel CPUE was positively associated with both deciduous ($\bar{x} = 23.7\%$, range = 14.79 – 30.66%) and evergreen ($\bar{x} = 19\%$, range = 11.12 – 31.24%) forest cover. Mussel H' was positively associated with percent wetland ($\bar{x} = 6\%$, range = 3.3 – 11.35%) and crop ($\bar{x} = 10.2\%$, range = 1.25 – 25.39%) coverage but negatively associated with mixed forest ($\bar{x} = 6.5\%$, range = 3.42 – 10.59%) and grassland ($\bar{x} = 6.3\%$, range = 3.88 – 8.79%) cover. Both mussel diversity and

richness were negatively associated with percent pasture cover (\bar{x} = 16%, range = 11.31 – 23.16%) at Coastal Plain sites.

High conservation concern mussels

The mean GHR for mussel assemblages in my study basins was >4 (Neuse = 4.36, Roanoke = 4.18, Tar = 4.10, Tables 2-4). Many Atlantic Slope mussels are geographically wide-ranging and most taxa are known from multiple, stable populations in several states with a few exceptions (e.g., *E. steinstanstana*, *P. collina*). Several formerly common and widespread mussels (e.g., *A. undulata*, *E. lanceolata*, *F. masoni*, *L. subviridis*, *S. undulatus*) have experienced localized (i.e., drainage-specific) declines and have substantially lower SHRs compared to GHRs. Although the average mussel assemblage SHR in my study basins was ≥ 3 (Neuse = 3.23, Roanoke = 3.34, Tar = 2.93, Tables 2-4) more than 79% of the individuals encountered were *E. complanata*. However, average mussel assemblage SHRs were lower when *E. complanata* were excluded from analyses (Neuse = 7% decrease, Roanoke = 28% decrease, Tar = 12% decrease from SHRs with *E. complanata*). Streams with intact dams had more S1 taxa ($n = 7$) than streams with breached ($n = 4$) and relict dams ($n = 5$). Streams with relict dams had no S2 species (*A. undulata* and *S. undulatus*).

In the Neuse Drainage, I found populations of S1 (*E. roanokensis*, *L. cariosa*) and S2 (*A. undulata*, *S. undulatus*) mussels in all three reaches associated with intact Wiggins Mill Dam on Contentnea Creek (Table 2). Upstream from Wiggin's Mill, two of three sites near the breached Buckhorn Dam had an S2 species (*A. undulata*). Surveys in the Little River revealed stable populations of an S1 species (*L. subviridis*) in the upstream and mill reaches of breached Mitchell Mill. I found a small population (1 male, 1 female) of an S2 species (*A.*

undulata) at the downstream site at the intact Lizard Lick Dam. Further downstream on the Little River, surveys at two relict dams (Cherry Hospital and Lowell's Mill) revealed populations of two S1 species (*E. roanokensis* and *L. radiata*, Table 2).

The upper Dan River in the Roanoke Basin (Table 3) holds populations of the only federally listed mussel species (*Pleurobema collina*, G1S1) found in the study ($n = 13$ individuals). *Pleurobema collina* was present in at least one reach at all study dams in the Dan River. Also in the upper Roanoke Basin, Mayo River surveys revealed an S1 species (*L. subviridis*) at 2/3 of intact Washington Mill study reaches. However, Dan River tributaries had few mussels or assemblages comprised of only 1-2 common species (*E. complanata* and *E. icterina*) with the exception of Long Mill's small population of an S2 species (*S. undulatus*).

Tar River Drainage streams contain numerous high conservation priority mussel taxa (Table 4). In Fishing Creek, I observed populations of five S1 species. In upper Fishing Creek, small populations of *Elliptio lanceolata* (S1) were found in all three reaches associated with relict Powell's Mill and Hamme's Mill downstream reach. Sites associated with intact Bellamy's Mill had four S1 species (*E. roanokensis*, *F. masoni*, *L. cariosa*, *L. radiata*) and one S2 species (*A. undulata*) and had an overall site mean SHR of 2.74 (Table 4). Two of three reaches associated with intact Laurel Mill in Sandy Creek contained populations of three S1 species (*E. roanokensis*, *F. masoni*, *L. radiata*). Headwaters of the Tar River contain a moderate amount of S1 (*F. masoni*, *L. radiata* ($n = 38$)) and S2 species (*A. undulata*) downstream of breached Day's Mill. Downstream in the Tar River at the Gooch's Mill upstream site, I found seven *F. masoni* (G2S1) along with 37 *Lampsilis n.s.* (status unknown). I found an S1 (*L. radiata*) and an S2 species (*S. undulatus*) at Gooch's

Mill mill reach. Breached Oxford City Dam had at least one S1 species in all three reaches (*L. cariosa*, *L. subviridis*). Relict Cannady's Mill upstream site surveys revealed a single *E. lanceolata* (S1) (Table 4). Two other S1 species (*E. roanokensis* and *L. cariosa*) were also found in study reaches. In the lower Tar River near Webb's Mill, three S1 species (*F. masoni*, *L. cariosa*, *L. subviridis*) and two S2 species (*A. undulata* and *S. undulatus*) were observed and the downstream reach produced the most diverse mussel assemblage with 10 taxa (Table 4).

DISCUSSION

My data suggest that streams with intact small dams frequently support dense, species-rich freshwater mussel assemblages. In contrast, many streams with breached or relict dams support highly variable mussel assemblages that are frequently less dense and diverse compared to those in nearby impounded streams. This phenomenon appears related to multiple factors that contribute to the stabilizing and moderating effects of small dams on streambed habitats, mussel food resources and growth conditions. Landuse may also have an important but context-dependent role in this association. Land cover data suggest that mussels respond to landuse attributes differently in the Piedmont and Coastal Plain physiographic provinces. Demographic data revealed larger mean and maximum *E. complanata* lengths in streams with intact dams suggesting more rapid growth and possibly higher recruitment levels. However, I found no evidence to support the hypothesis that dam-mediated fish host aggregation is linked to mussel aggregations associated with small dams. Taken together these data suggest that small intact dams in eastern North Carolina provide benefits for freshwater mussel populations and sustain healthy populations.

Dam effects on bivalve assemblages

Mill reaches in streams with intact dams had significantly higher mussel CPUE and density compared to up-and-downstream reaches. In addition, abundance and mean length of the dominant mussel taxon, *Elliptio complanata* were both greater in mill reaches of intact

dams compared to up-and-downstream reaches. Mussel abundance and richness were lowest in streams with relict dams suggesting that recovery (i.e., recruitment and re-colonization) following dam breaching is a long-term process. Mussel abundance patterns at breached sites were equivocal and mirror results of the only other study of the effects (short-term) on mussel assemblages (Sethi et al. 2004). I found that mussel abundance was highest in the downstream reaches (>500 m) of breached dams. These patterns mirror those observed in Alabama streams (Gangloff et al. 2011) and provide further evidence that uncontrolled breaching of small intact dams may have profound negative effects on native bivalve populations.

Small dams also appear to benefit other bivalves. Streams with intact dams had higher *C. fluminea* density compared to streams with breached or relict dams. *C. fluminea* and mussel density were strongly correlated but *C. fluminea* densities were more variable whereas unionid densities ranged from 0-5 mussels/m². These data may indicate that density coexistence threshold exists for unionids and *C. fluminea* or that I sampled over a limited range of mussel densities. Samples from very high density (i.e., >5 individuals/m²) mussel sites should yield more insight into spatial limits and habitat effects on structure and composition of native/invasive freshwater bivalve aggregations.

Dam effects on mussel host fish

Because larval mussels are briefly parasitic on fishes, their distribution may be linked to host-fish dispersal (Watters 1992). Mussel larvae may be generalists that use a diverse range of fish taxa as hosts or specialists that use only one or few closely related species (Watters 1994; Haag & Warren 1998). Abundant, widespread mussel species may use either

more common fish species as hosts, use more than one fish species, or both (Vaughn & Taylor 2000). Patterns of host fish use among mussel species may help elucidate patterns of mussel distribution and abundance in some streams. I observed no significant differences in mussel host fish metrics between reaches at any dam types in my study streams. Yet, there was a positive significant relationship between percentage of known mussel host fish and mussel CPUE.

Surprisingly, breached dams had the highest percentage of known host fishes (primarily centrarchids and other taxa known to serve as hosts for a broad range of mussel taxa, see Watters 1994 and Williams et al. 2008) at my sites contradicting the hypothesis that intact dam mill reaches have higher host-fish abundance because dams aggregate host fishes. Recently, Helms et al. (2011) reported no evidence that small dams promote aggregation of Alabama stream fishes. Fish assemblages at my study sites were comprised of mostly resident (i.e., non-migratory) fish taxa. American eel (*Anguilla rostrata*) was the only migratory (catadromous) species frequently encountered. Further, many mussel species encountered at my study sites are generalists and have >5 fish taxa that are host fish with the exception of a few uncommon species (e.g., *E. lanceolata*, *E. steinstansana*) (Watters 1994; Chris Eads, personal communication). Alternatively, some taxa including *L. subviridis* and *U. imbecillis* by-pass host-fish parasitism and utilize direct transformation in the marsupial of the female (Barfield & Watters 1998; Lellis & King 1998).

Dam effects on habitat

Streams with intact dams had substrates comprised of a higher percentage of gravel and cobble particles, bedrock, wood and clay compared to breached or relict dams. Streams

with breached dams had a higher percentage of sand and silt and fewer gravel and cobble particles compared to intact dams. Further, downstream reaches of breached dams had 5% more sand compared to intact dam downstream reaches. These findings suggest that small intact dams may not only entrain sand and silt but also increase channel and substrate stability of reaches downstream of the dam. Substrate associations were somewhat counter-intuitive and indicate that the effects of small dams on stream habitats are complex.

Gangloff et al. (2011) first proposed that mill reach habitats may represent relict habitats that are essentially un-changed from prevailing conditions at the time of dam construction (typically 1800s-1920s). Streambed stability is generally believed to be a key trait of most optimal mussel habitats (Strayer & Ralley 1993; McRae et al. 2004) and the hyper-stable substrates typifying many mill reaches support very high-density (>50 individuals/m²) unionid aggregations (Gangloff et al. 2009a).

My data suggest that the negative effects of dam breaching are considerable on mussel populations and their habitats immediately downstream (0-150 m) of the dam. However, mechanisms for negative effects of dam breaching on downstream (>0.5 km) mussel populations in my study are hard to decipher due to either A) the lack of pre-breach data to quantify effects on resident mussel populations or B) the stream is in a state of rebound (i.e., mussels have begun to re-colonize reaches downstream from the dam site). A small dam breaching in a Wisconsin stream affected mussel populations >1 km downstream over a three year period (Sethi et al. 2004). During and for a considerable time following dam removal, sediment stored in the impoundment is released downstream. The rate at which these particles move depends on the amount and size of the sediment as well as stream discharge (Pizzuto 2002). Breaching effects on mussels may take years to observe because

many species grow slowly and recruit infrequently. In addition, effects of disturbance may not be apparent until mussels fail to reproduce or recruit (McMahon & Bogan 2001; Sethi et al. 2004). However, unionids appear able to tolerate short sediment pulses (Brim-Box & Mossa 1999; Gangloff et al. 2009b).

Fish and macroinvertebrate populations respond quickly following dam breaching or removal (Stanley et al. 2002; Maloney et al. 2008), however this could be due to the high mobility (fish) or short life cycles (macroinvertebrates) of these organisms which allows them to rapidly re-colonize after habitat modification (Sethi et al. 2004). Freshwater mussels should be far slower due to their low dispersal rates. Recovery of mussel populations may occur after reservoir sediments move through the system, however in low-to moderate-gradient Piedmont and Coastal Plain streams, recovery may take decades.

Removal of dams like Lowell Mill Dam on the Little River in 2005 resulted in increased use of formerly impounded reaches by migratory and resident fish taxa (Raabe & Hightower 2008) and increased abundance and diversity of freshwater mussels within the former impoundment 3-4 y after removal (T. Savidge, Catena Group, personal communication). My surveys revealed that a moderately dense ($\bar{x} = 3.75$ mussels/m²) and species-rich (\bar{x} richness = 4 taxa per transect) mussel assemblage is extant near the restored Lowell Mill Dam site 6 y later. However, my surveys failed to reveal any federally-listed mussels that once inhabited this section of the stream (i.e., *E. steinstansana*). Without knowledge of exact date of dam breaching or ecological studies documenting effects, it is difficult to directly infer the stream and biotic responses to dam breaching or removal.

Dam effects on water temperature

Impoundments with surface-release dams elevate water temperatures and particulate organic matter (POM) export to downstream communities (Webster et al. 1979; Lessard & Hayes 2003). Freshwater mussels are critical processors of POM (Monaghan et al. 2001) and elevated POM rates have long been known to benefit filter-feeding macroinvertebrates (Cushing 1963). Increased water temperatures observed downstream from an intact dam in Alabama enhanced food resources (i.e., algae, bacteria, plankton, POM, DOM) for downstream mussel populations (Singer & Gangloff 2011). Mussel shell growth rate is strongly affected by environmental conditions including water temperature, pH, conductivity and food availability (Soldati et al. 2009). Because mussel lifespan and maximum size are limited by colder temperatures (Bauer 1992), warmer temperatures promote faster shell growth and are more suitable for food production. Quadrat excavations revealed that intact dam mill reaches had more *Elliptio complanata* > 100 mm in length than conspecifics up-or-downstream suggesting that mill reach mussels of intact dams are growing faster than conspecifics located up-or downstream. Singer and Gangloff (2011) found *Elliptio arca* were growing faster immediately below an intact dam in Alabama and were larger at ages 5-7 years compared to mussels found up-and downstream of the dam. My data indicate similar trends in North Carolina streams with intact dams.

Effect of landuse on bivalve assemblages

Historical and current landuse may provide further insight into the mussel assemblage patterns observed in my study. On average, study sites were moderately forested (3.01 – 61.58%) with deciduous forest representing the dominant forest type. However, rapid, recent

increases in human populations and development within the North Carolina Piedmont have contributed to stream habitat and water quality degradation (Doll et al. 2002). Positive correlations between mussel richness or diversity and the percentage of total urban land cover highlight the on-going process of urban sprawl across high diversity watersheds in eastern North Carolina. Humans have contributed to the decline of mussel species globally; however regional effects of urban intensity may not be apparent for some time.

Many of my sites are in close-proximity to areas affected by beaver (*Castor canadensis*) suggesting that positive correlations between mussel assemblage metrics and the percentage of wetland cover within the catchment may indicate beneficial effects of beavers on mussels in Piedmont stream ecosystems. A cycle of field abandonment and new land clearing left North Carolina Piedmont landscapes an irregular patchwork of fields and forested areas (Oosting 1942). Presently, early-successional species like loblolly pine (*Pinus taeda*) and shortleaf pine (*P. echinata*) dominate many North Carolina Piedmont upland forests (McDonald et al. 2002). This is primarily the result of this large-scale clearing and subsequent land abandonment and forest regeneration (Taverna et al. 2004). Hardwood plots would have only persisted in high-gradient slopes and other areas difficult to cultivate. Less easily cultivated areas would have been abandoned first and left to grow back into early successional pine stands (Oosting 1942). The highest quality agricultural fields would have remained in production. Thus, negative associations between mussel assemblage metrics and percent deciduous forest cover could also be linked to historical land use change associated with constant land clearing and abandonment. This contrasts with the positive relationships found between mussel parameters and evergreen forest cover. In addition, the positive associations between mussel diversity and richness and percentage of crop, pasture, wetland

and grass surface cover may indicate open stream canopies and thus increased allochthonous mussel food production (Morris & Corkum 1996).

Implications for dam removal

There has been an increased interest in removing dams, with a growing number of removals occurring in North Carolina (Burdick & Hightower 2006; Riggsbee et al. 2007). Dam removal projects are considered on a case-by-case basis in North Carolina by the Dam Removal Task Force (www.saw.usace.army.mil/WETLANDS/Library/index.html) and removals for mitigation credit generally apply to larger dams on channels with widths > 20 ft. If the removal project does not meet at least two of the four general criteria outlined by the US Army Corps of Engineers and NC Division of Water Quality, in conjunction with other Federal and State agencies, then it is unlikely the project will have the support for compensatory mitigation from those agencies. The general criteria are A) water quality issues, B) rare, endangered and threatened aquatic species, C) establishment of an appropriate aquatic community, and D) anadromous fish passage. Data from my project can be used, in conjunction with other information, to address three of the four issues and aid agencies tasked with decisions regarding dam removal prioritization.

Taken together, results of my research suggest that small dams may frequently have strong counter-intuitive positive effects on mussel population persistence and species richness. Mussel assemblage persistence appears to be a result of complex interactions between biotic and abiotic factors across multiple spatial and temporal scales. These small, older structures appear to foster the establishment of large mussel populations most likely due to channel stabilization or food augmentation. Although dam removal likely has long-

term restorative benefits (i.e., stream connectivity), removal projects need to examine the trade-offs between ecological costs and benefits. Removal could be detrimental to imperiled mussel populations and habitats downstream of the dam, thus positive and negative impacts of removal need to be considered for effective resource decisions regarding imperiled taxa.

REFERENCES

- Barfield, M. L., and G. T. Watters. 1998. Non-parasitic life cycle in the green floater, *Lasmigona subviridis* (Conrad, 1835). *Triannual Unionid Report* **16**:22.
- Bauer, G. 1992. Variation in the life span and size of the freshwater pearl mussel. *Journal of Animal Ecology* **61**:425-436.
- Baxter, R. M. 1977. Environmental effects of dams and impoundments. *Annual Review of Ecology and Systematics* **8**:255-283.
- Benke, A. C. 1990. A perspective on America's vanishing streams. *Journal of the North American Benthological Society* **9**:77-88.
- Bogan, A. E. 2007. Workbook and key to the freshwater bivalves of North Carolina. North Carolina Freshwater Mussel Conservation Partnership, Raleigh, NC. 105 pp.
- Bogan, A. E. 2008. Global diversity of freshwater mussels (Mollusca, Bivalvia) in freshwater. *Hydrobiologia* **595**:139-147.
- Brim-Box, J., and J. Mossa. 1999. Sediment, land use, and freshwater mussels: prospects and problems. *Journal of the North American Benthological Society* **18**:99-117.
- Burdick, S. M., and J. E. Hightower. 2006. Distribution of spawning activity by anadromous fishes in an Atlantic Slope drainage after removal of a low-head dam. *Transactions of the American Fisheries Society* **135**:1290-1300.
- Clarke, A. H. 1986. Competitive exclusion of *Canthyria* (Unionidae) by *Corbicula fluminea* (Muller). *Ecosearch Series* **1**:3-10.

- Clarke, A. H. 1988. Aspects of corbiculid-unionid sympatry in the United States. *Ecoscience* Series **2**:57-99.
- Counts, C. L. 1986. The zoogeography and history of the invasion of the United States by *Corbicula fluminea* (Bivalvia: Corbiculidae). *American Malacological Bulletin* Special Edition **2**:7-9.
- Cushing, C. E. Jr. 1963. Filter-feeding insect distribution and planktonic food in the Montreal River. *Transactions of the American Fisheries Society* **92**:216-219.
- Dam Removal Task Force. 2008. Determining appropriate compensatory mitigation credit for dam removal projects in North Carolina. US Army Corps of Engineers Wilmington District, US Environmental Protection Agency Region 4, US Fish and Wildlife Service, North Carolina Division of Water Quality, North Carolina Wildlife Resources Commission, and North Carolina Division of Water Resources. Available from <http://www.saw.usace.army.mil/WETLANDS/Library/index.html> (accessed January 2012).
- Dean, J., D. Edds, D. Gillette, J. Howard, S. Sherraden, and J. Tiemann. 2002. Effects of lowhead dams on freshwater mussels in the Neosho River, Kansas. *Transactions of the Kansas Academy of Science* **105**:232-240.
- DeLorme Map. 2003. North Carolina Atlas and Gazetteer. Yarmouth, Maine.
- Doll, B. A., D. E. Wise-Frederick, C. M. Buckner, S. D. Wilkerson, W. A. Harman, R. E. Smith, and J. Spooner. 2002. Hydraulic geometry relationships for urban streams throughout the Piedmont of North Carolina. *Journal of the American Water Resources Association* **38**:641-651.
- Doyle, M. W., E. H. Stanley, and J. M. Harbor. 2003. Channel adjustments following two

- dam removals in Wisconsin. *Water Resources Research* **39**:1-15.
- Gangloff, M. M., E. E. Hartfield, E. E. Singer, B. Helms, D. Werneke, K. White, and J. W. Feminella. 2009a. Alabama Mill Dam Inventory Report. Alabama Department of Conservation and Natural Resources, Montgomery, Alabama.
- Gangloff, M. M., L. M. Siefferman, W. A. Seesock, and C. W. Webber. 2009b. Effects of urban tributaries on freshwater mussel abundance in a biologically diverse piedmont (USA) stream. *Hydrobiologia* **636**:191-201.
- Gangloff, M. M., E. E. Hartfield, D. C. Werneke, and J. W. Feminella. 2011. Associations between small dams and mollusk assemblages in Alabama streams. *The Journal of North American Benthological Society* **30**:1107-1116.
- Graf, W. L. 1999. Dam Nation: a geomorphic census of American dams and their large-scale hydrologic impacts. *Water Resources Research* **35**:1305-1311.
- Graf, W. L. 2005. Geomorphology and American dams: the scientific, social, and economic context. *Geomorphology* **71**:3-26.
- Graf, W. L. 2006. Downstream hydrologic and geomorphic effects of large dams on American rivers. *Geomorphology* **79**:336-360.
- Graf, W. L., J. J. Boland, D. Dixon, T. C. Downs, J. Kraeuter, M. L. Soscia, D. L. Wegner, P. B. Williams, C. S. Wingo, and E. P. Zeisel. 2002. Dam removal: science and decision making. The Heinz Center, Washington, D.C.
- Haag, W. R. 2010. A hierarchical classification of freshwater mussel diversity in North America. *Journal of Biogeography* **37**:12-26.
- Haag, W. R., and M. L. Warren, Jr. 1998. Role of ecological factors and reproductive strategies in structuring freshwater mussel communities. *Canadian Journal of*

- Fisheries and Aquatic Sciences **55**:297-306.
- Hakenkamp, C. C., S. G. Ribblett, M. A. Palmer, C. M. Swan, J. W. Reid and M. R. Goodison. 2001. The impact of an introduced bivalve (*Corbicula fluminea*) on the benthos of a sandy stream. *Freshwater Biology* **46**:491-501.
- Hannan, H. H. 1979. Chemical modifications in reservoir-regulated streams. Pages 75-95 in Ward, J. V. and J. A. Stanford, editors. *The Ecology of Regulated Streams*. Plenum, New York, New York.
- Hebblewhite, M., C. A. White, C. G. Nietvelt, J. A. McKenzie, T. E. Hurd, J. M. Fryxell, S. E. Bayley, and P. C. Paquet. 2005. Human activity mediates a trophic cascade caused by wolves. *Ecology* **86**:2135-2144.
- Hedges, L. V., J. Gurevitch, and P. S. Curtis. 1999. The meta-analysis of response ratios in experimental ecology. *Ecology* **80**:1150-1156.
- Helms, B. S., D. C. Werneke, M. M. Gangloff, E. E. Hartfield, and J. W. Feminella. 2011. The influence of low-head dams on fish assemblages in streams across Alabama. *Journal of the North American Benthological Society* **30**:1095-1106.
- Jansson, R., C. Nilsson, and B. Renofalt. 2000. Fragmentation of riparian floras in rivers with multiple dams. *Ecology* **81**:899-903.
- Jenkins, S. H., and P. E. Busher. 1979. *Castor canadensis*. *Mammalian Species* **120**:1-9.
- Kat, P. W. 1984. Parasitism and the Unionacea (Bivalvia). *Biological Reviews* **59**:189-207.
- Kraemer, L. K. 1979. *Corbicula* (Bivalvia: Sphaeriacea) vs. indigenous mussels (Bivalvia: Unionacea) in U.S. rivers: a hard case for interspecific competition? *American Zoologist* **19**:1085-1096.
- Lellis, W. A., and T. L. King. 1998. Release of metamorphosed juveniles by the green

- floater, *Lasmigona subviridis*. Triannual Unionid Report **16**:23.
- Lessard, J. L., and D. B. Hayes. 2003. Effects of elevated water temperature on fish and macroinvertebrate communities below small dams. *River Research and Applications* **19**:721-732.
- Levin, S. A. 1992. The problem of pattern and scale in ecology: The Robert H. MacArthur Award Lecture. *Ecology* **73**:1943-1967.
- Lydeard, C., R. H. Cowie, W. F. Ponder, A. E. Bogan, P. Bouchet, S. A. Clark, K. S. Cummings, T. J. Frest, O. Gargominy, D. G. Herbert, R. Hershler, K. E. Perez, B. Roth, M. Seddon, E. E. Strong, and F. G. Thompson. 2004. The global decline of nonmarine mollusks. *BioScience* **54**:321-330.
- Maloney, K. O., H. R. Dodd, S. E. Butler, and D. H. Wahl. 2008. Changes in macroinvertebrate and fish assemblages in a medium-sized river following a breach of a low-head dam. *Freshwater Biology* **53**:1055-1068.
- McDonald, R. I., R. K. Peet, and D. L. Urban. 2002. Environmental correlates of oak decline and red maple increase in the North Carolina Piedmont. *Castanea* **67**:84-95.
- McMahon, R. F., and A. E. Bogan. 2001. Mollusca:Bivalvia. Pages 331-430 in J. H. Thorp and A. P. Covich, editors. *Ecology and Classification of North American Freshwater Invertebrates*. 2nd edition. Academic Press, San Diego, California.
- McRae, S. E., J. D. Allan, and J. B. Burch. 2004. Reach-and catchment-scale determinants of the distribution of freshwater mussels (Bivalvia: Unionidae) in south-eastern Michigan, U.S.A. *Freshwater Biology* **49**:127-142.
- Miller, A. C., and B. S. Payne. 1993. Qualitative versus quantitative sampling to evaluate population and community characteristics at a large-river mussel bed. *American*

- Midland Naturalist **130**:133-145.
- Miller, A. C., and B. S. Payne. 1994. Co-occurrence of native freshwater mussels (Unionidae) and the non-indigenous *Corbicula fluminea* at two stable shoals in the Ohio River, U.S.A. *Malacological Review* **27**:87-97.
- Monaghan, M. T., S. A. Thomas, G. W. Minshall, J. D. Newbold, and C. E. Cushing. 2001. The influence of filter-feeding benthic macroinvertebrates on the transport and deposition of particulate organic matter and diatoms in two streams. *Limnology and Oceanography* **46**:1091-1099.
- Morris, T. J., and L. D. Corkum. 1996. Assemblage structure of freshwater mussels (Bivalvia: Unionidae) in rivers with grassy and forested riparian zones. *Journal of the North American Benthological Society* **15**:576-586.
- Naiman, R. J., C. A. Johnston, and J. C. Kelley. 1988. Alteration of North American streams by beaver. *BioScience* **38**:753-762.
- Neraas, L. P., and P. Spruell. 2001. Fragmentation of riverine systems: the genetic effects of dams on bull trout (*Salvelinus confluentus*) in the Clark Fork River system. *Molecular Ecology* **10**:1153-1164.
- Neves R. J., A. E. Bogan, J. D. Williams, S. A. Ahlstedt, and P. W. Hartfield. 1997. Status of aquatic mollusks in the southeastern United States: A downward spiral of diversity. Pages 43-86 in G. W. Benz and D. E. Collins, editors. *Aquatic Fauna in Peril: The Southeastern Perspective*. Special Publication 1, Southeast Aquatic Research Institute, Lenz Design and Communications, Decatur, Georgia.
- Obermeyer, B. K. 1997. A comparison of quadrats versus timed snorkel searches for assessing freshwater mussels. *American Midland Naturalist* **139**:331-339.

- Oosting, H. J. 1942. An ecological analysis of the plant communities of Piedmont, North Carolina. *American Midland Naturalist* **28**:1–126.
- Parmalee, P. W., and A. E. Bogan. 1998. The freshwater mussels of Tennessee. University of Tennessee Press, Knoxville, Tennessee. 328 pp.
- Petts, G. E. 1984. The Impounded River. Pages 1-25 in G. E. Petts. *Impounded Rivers*. John Wiley and Sons, Chichester, United Kingdom.
- Pizzuto, J. 2002. Effects of dam removal on river form processes. *BioScience* **52**:683-691.
- Poff, N. L., and D. Hart. 2002. How dams vary and why it matters for the emerging science of dam removal. *BioScience* **52**:659-668.
- Powell, M. B., P. Hervey, B. Wilson, D. Salvesen, and D. Godschalk. 2003. The impacts of growth and sprawl in North Carolina Report. North Carolina Rural Economic Development Center, The University of North Carolina at Chapel Hill, Chapel Hill, North Carolina.
- Raabe, J. K., and J. E. Hightower. 2008. Assessing benefits to migratory fishes of habitat restored by dam removal annual report. U. S. Geological Survey, North Carolina State University, Raleigh, North Carolina.
- Ricciardi, A. L., and J. B. Rasmussen. 1999. Extinction rates of North American freshwater fauna. *Conservation Biology* **13**:1220-1222.
- Riggsbee, J. A., J. P. Julian, M. W. Doyle, and R. G. Wetzel. 2007. Suspended sediment, dissolved organic carbon, and dissolved nitrogen export during the dam removal process. *Water Resources Research* **43**:1-16.
- Schmitz, O. J., P. A. Hamback, and A. P. Beckerman. 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *The American*

- Naturalist **155**:141-153.
- Sethi, S. A., A. R. Selle, M. W. Doyle, E. H. Stanley, and H. E. Kitchel. 2004. Response of unionid mussels to dam removal in Koshkonong Creek, Wisconsin (USA).
Hydrobiologia **525**:157-165.
- Shannon, C. E. and Weaver, W. 1949. The mathematical theory of communication.
University of Illinois Press, Urbana.
- Simpson, E. H. 1949. Measurement of diversity. Nature **163**:688.
- Singer, E. E., and M. Gangloff. 2011. Effects of a small dam on freshwater mussel growth in an Alabama (U.S.A) stream. Freshwater Biology **56**:1904-1915.
- Smith, D. G. 1985. Recent range expansion of the freshwater mussel, *Anodonta implicata*, and its relationship to clupeid fish restoration in the Connecticut river system.
Freshwater Invertebrate Biology **4**:105-108.
- Soldati, A. L., D. E. Jacob, B. R. Schone, M. M. Bianchi, and A. Hadjuck. 2009. Seasonal periodicity of growth and composition in valves of *Diplodan chilensis patagonicus* (D'Orbigny, 1835). Journal of Molluscan Studies **75**:75-85.
- Stanley, E. H., and M. W. Doyle. 2002. A geomorphic perspective on nutrient retention following dam removal. BioScience **52**:693-701.
- Stanley, E. H., M. A. Luebke, M. W. Doyle, and D. W. Marshall. 2002. Short-term changes in channel form and macroinvertebrate communities following low-head dam removal. Journal of the North American Benthological Society **21**:172-187.
- Strayer, D. L. 1999. Effects of alien species on freshwater mollusks in North America.
Journal of the North American Benthological Society **18**:74-98.
- Strayer, D. L. 2008. Freshwater Mussel Ecology: A Multifactor Approach to Distribution

- and Abundance. Freshwater Ecology Series, Berkeley and Los Angeles, California.
- Strayer, D. L. and J. Ralley. 1993. Microhabitat use by an assemblage of stream-dwelling Unionaceans (Bivalvia), including two rare species of *Alasmidonta*. Journal of the North American Benthological Society **12**:247-258.
- Strayer D. L., J. A. Downing, W. R. Haag, T. L. King, J. B. Layzer, T. J. Newton, and S. J. Nichols. 2004. Changing perspectives on pearly mussels, North America's most imperiled animals. BioScience **54**:429-439.
- Taverna, K., D. L. Urban, and R. I. McDonald. 2004. Modeling landscape vegetation pattern in response to historic land-use: a hypothesis-driven approach for the North Carolina Piedmont, USA. Landscape Ecology **20**:689-702.
- Tiemann, J. S., D. P. Gillette, M. L. Wildhaber, and D. R. Edds. 2004. Effects of lowhead dams on riffle-dwelling fishes and macroinvertebrates in a Midwestern river. Transactions of the American Fisheries Society **133**:705-717.
- Tiemann, J. S., H. R. Dodd, N. Owens, and D. H. Wahl. 2007. Effects of lowhead dams on Unionids in the Fox River, Illinois. Northeastern Naturalist **14**:125-138.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences **37**:370-377.
- Vaughn, C. C. 1997. Regional patterns of mussel distributions in North American rivers. Ecography **20**:107-115.
- Vaughn, C. C., C. M. Taylor, and K. J. Eberhard. 1997. A comparison of the effectiveness of times searches vs. quadrat sampling in mussel surveys. In: Conservation and Management of Freshwater Mussels II: Proceedings of a UMRCC Symposium pp.

157-162.

- Vaughn, C. C., and C. M. Taylor. 1999. Impoundments and the decline of freshwater mussels: a case study of an extinction gradient. *Conservation Biology* **13**:912-920.
- Vaughn, C. C., and C. M. Taylor. 2000. Macroecology of a host-parasite relationship. *Ecography* **23**:11-20.
- Vaughn, C. C. and D. E. Spooner. 2006. Scale-dependent associations between native freshwater mussels and invasive *Corbicula*. *Hydrobiologia* **568**:331-339.
- Vaughn, C. C., S. J. Nichols, and D. E. Spooner. 2008. Community and foodweb ecology of freshwater mussels. *Journal of American Benthological Society* **27**:409-423.
- Walter, R. C., and D. J. Merritts. 2008. Natural streams and the legacy of water-powered mills. *Science* **319**:299-204.
- Ward, J. V., and J. A. Stanford. 1979. Ecological factors controlling stream zoobenthos with emphasis on thermal modification of regulated streams. Pages 35-56 in J. V. Ward and J. A. Stanford, editors. *The Ecology of Regulated Streams*. Plenum, New York, New York.
- Watters, G. T. 1992. Unionids, fishes, and the species-area curve. *Journal of Biogeography* **19**:481-490.
- Watters, G. T. 1994. An annotated bibliography of the reproduction and propagation of the Unionoidea (primarily of North America). *Ohio Biological Survey of Miscellaneous Contributions* **1**:1-158.
- Watters, G. T. 1996. Small dams as barriers to freshwater mussels (*Bivalvia*, *Unionoidea*) and their hosts. *Biological Conservation* **75**:79-85.
- Watters, G. T. 2001. The evolution of the Unionacea in North America, and its implications

- for the worldwide fauna. Pages 281-307 in G. Bauer and K. Wachtler, editors.
Ecology and Evolution of the Freshwater Mussel Unionoida. Springer, New York.
- Webster, J. R., E. F. Benfield, and J. Cairns Jr. 1979. Model predictions of impoundments on particulate organic matter transport in a river system. Pages 257-272 in J. V. Ward and J. A. Stanford, editors. The Ecology of Regulated Streams. Plenum, New York, New York.
- Wilcove, D. S., and L. L. Master. 2005. How many endangered species are there in the United States? *Frontiers in Ecology and the Environment* **3**:414-420.
- Williams, J. D., M. L. Warren, Jr., K. S. Cummings, J. L. Harris, and R. J. Neves. 1993. Conservation status of freshwater mussels of the United States and Canada. *Fisheries* **18**:6-22.
- Williams, J. D., A. E. Bogan, and J. T. Garner. 2008. *Freshwater Mussels of Alabama and the Mobile Basin in Georgia, Mississippi and Tennessee*. University of Alabama Press, Tuscaloosa, AL. 908 pp.
- Wolman, M. G. 1954. A method of sampling coarse river-bed material. *Transactions, American Geophysical Union* **35**:951-956.
- Yamamoto, S., K. Morita, I. Koizumi, and K. Maekawa. 2004. Genetic differentiation of white-spotted char (*Salvelinus leucomaenis*) populations after habitat fragmentation: spatial-temporal changes in gene frequencies. *Conservation Genetics* **5**:529-538.

FIGURES

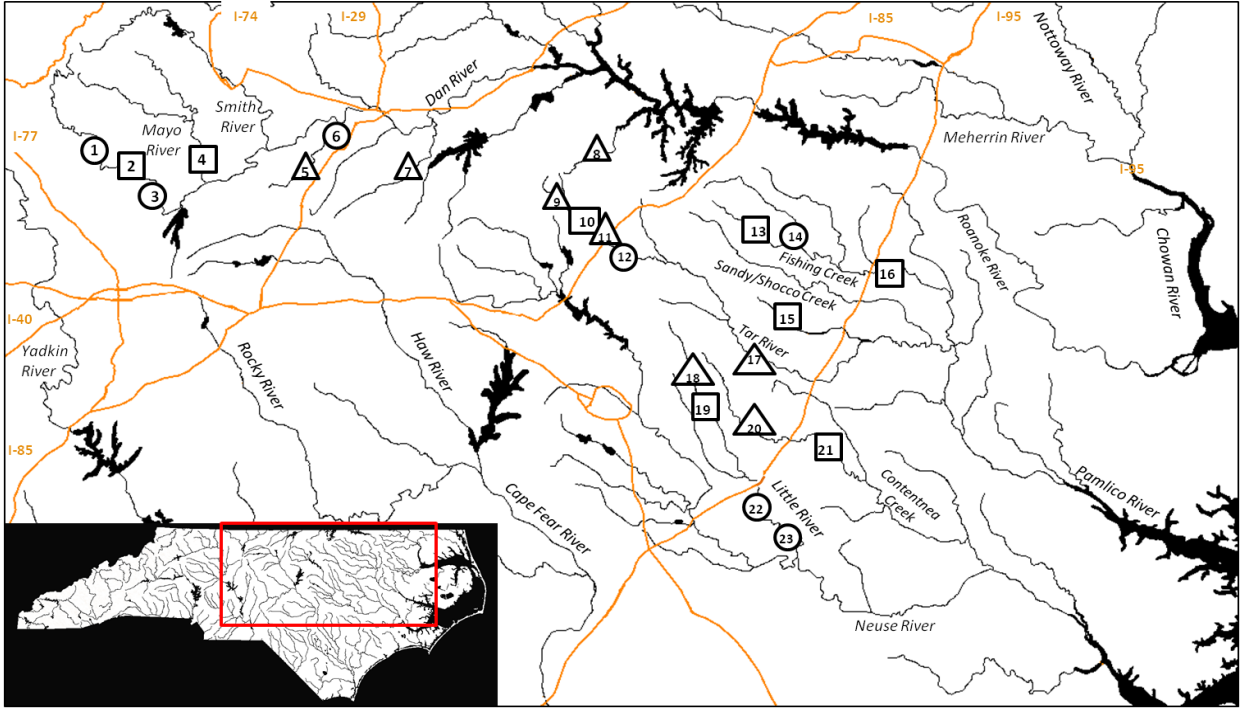


Figure 1. Map of study sites in east-central North Carolina. Intact dams indicated by rectangles, breached dams by triangles and relict dams by ellipses. Dam site numbers correspond to numbers in Table 1.

Table 1. List of dams, river drainage, physiographic region, study stream, dam status and coordinates of dam or former dam sites in east-central North Carolina. Dam site numbers correspond to numbered symbols in Figure 1.

Dam	Drainage	Physiographic Region	Stream	Status	Latitude	Longitude
1. Joyce	Roanoke	Piedmont	Dan River	Relict	36.53711	-80.40073
2. Jessup		Piedmont	Dan River	Intact	36.52686	-80.37380
3. George's		Piedmont	Dan River	Relict	36.51576	-80.30387
4. Washington		Piedmont	Mayo River	Intact	36.41800	-79.96292
5. Worsham		Piedmont	Wolf Island Cr.	Breached	36.45244	-79.57024
6. Chandler		Piedmont	Wolf Island Cr.	Relict	36.51563	-79.51764
7. Long		Piedmont	Country Line Cr.	Breached	36.46540	-79.21368
8. Dalton		Piedmont	Grassy Cr.	Breached	36.49060	-78.61629
9. Days	Tar	Piedmont	Tar River	Breached	36.32037	-78.76478
10. Gooch's		Piedmont	Tar River	Intact	36.29269	-78.70781
11. Oxford City		Piedmont	Tar River	Breached	36.26756	-78.66902
12. Cannady's		Piedmont	Tar River	Relict	36.19041	-78.55904
13. Hamme's		Coastal Plain	Fishing Cr.	Intact	36.36908	-78.15382
14. Powell		Coastal Plain	Fishing Cr.	Relict	36.33895	-78.12939
15. Laurel		Coastal Plain	Sandy Cr.	Intact	36.17804	-78.19111
16. Bellamy		Coastal Plain	Fishing Cr.	Intact	36.15500	-77.74274
17. Webb		Coastal Plain	Tar River	Breached	35.93617	-78.14868
18. Mitchell	Neuse	Piedmont	Little River	Breached	35.91402	-78.38745
19. Lizard Lick		Piedmont	Little River	Intact	35.82253	-78.35219
20. Buckhorn		Coastal Plain	Contentnea Cr.	Breached	35.69789	-78.06197
21. Wiggin's		Coastal Plain	Contentnea Cr.	Intact	35.68800	-77.94872
22. Lowell		Piedmont	Little River	Relict	35.56589	-78.16013
23. Cherry		Coastal Plain	Little River	Relict	35.39387	-78.02666

Table 2. Mussel assemblage metrics from sites within the Neuse River Drainage. I = intact dam, B = breached dam, R = relict dam. US = upstream reach, Mill = mill reach, DS = downstream reach of the dam.

Mussel Taxa	Dam	Wiggins Mill (I)			Buckhorn Mill (B)			Mitchell Mill (B)			Cherry Hospital (R)			Lowell Mill (R)			Lizard Lick Mill (I)		
	Stream	Contentnea Creek			Contentnea Creek			Little River			Little River			Little River			Little River		
	Reach	US	Mill	DS	US	Mill	DS	US	Mill	DS	US	Mill	DS	US	Mill	DS	US	Mill	DS
<i>Alasmidonta undulata</i>		1		1	1	1													2
<i>Elliptio complanata</i>		182	398	409	45	403	122	211	47	71	257	85	374	437	1033	1804	160	227	316
<i>Elliptio cistellaformis</i>									20		16	9	86				10	66	20
<i>Elliptio congaraea</i>		14	1	21	3		10				2			1	4	8		7	3
<i>Elliptio fisheriana</i>		6	9		9	28	2		2	2					5	2	5	22	2
<i>Elliptio icterina</i>			1	44	12	402	30	78	47	43	38	7	48	128	48	100	176	123	369
<i>Elliptio icterina/cistellaformis</i>		142																	
<i>Elliptio mediocris</i>				57															
<i>Elliptio roanokensis</i>			8	2							6	64			1				
<i>Lampsilis radiata</i>		1	5	7									2	1					
<i>Lasmigona subviridis</i>								3	6										
<i>Pyganodon cataracta</i>			59	8		3		16											
<i>Strophitus undulatus</i>			1																
<i>Utterbackia imbecillis</i>			46																
Total Taxa		6	9	8	5	5	4	4	5	3	4	4	5	4	4	5	4	5	6
Total Mussels		346	528	549	70	837	164	308	122	116	313	107	574	567	1090	1915	351	445	712
Mean Diversity (H')		0.84	0.72	0.83	0.53	0.59	0.55	0.65	0.64	0.39	0.47	0.35	0.89	0.57	0.25	0.23	0.76	0.83	0.72
Mean Diversity (1-D)		0.55	0.41	0.43	0.55	0.54	0.41	0.47	0.68	0.49	0.31	0.36	0.53	0.36	0.10	0.11	0.54	0.64	0.53
Total Search Effort (hrs)		15.62	20.62	13.02	14.33	15.82	11.13	7.20	12.82	8.72	7.13	4.50	8.00	13.03	12.72	11.30	7.18	10.58	7.15
Mean CPUE		20.74	27.78	41.64	4.44	51.16	14.52	35.20	8.87	11.42	40.50	23.00	65.45	45.01	73.51	157.20	49.10	37.73	95.08
Mean G-Rank		4.33	4.44	4.29	4.20	4.60	4.25	4.50	4.25	4.67	4.33	4.33	4.50	4.50	4.25	4.00	4.67	4.25	4.20
Mean S-Rank		2.67	3.11	2.86	3.20	3.60	3.50	3.50	3.00	3.67	3.67	3.00	2.50	3.00	3.50	3.00	3.67	3.50	3.20

Table 3. Mussel assemblage metrics from sites within the Roanoke River Drainage. I = intact dam, B = breached dam, R = relic dam. US = upstream reach, Mill = Mill reach, DS = downstream reach of the dam.

Mussel Taxa	Dam Stream Reach	Long's Mill (B)			Dalton Mill (B)			Worsham Mill (B)			Chandler Mill (R)			Jessup's Mill (I)			George's Mill (R)			Joyce's Mill (R)			Washington Mill (I)		
		Country Line Creek			Grassy Creek			Wolf Island Creek			Wolf Island Creek			Dan River			Dan River			Dan River			Mayo River		
		US	Mill	DS	US	Mill	DS	US	Mill	DS	US	Mill	DS	US	Mill	DS	US	Mill	DS	US	Mill	DS	US	Mill	DS
<i>Elliptio complanata</i>		302	145	302		234	845						979	573	152	64	89	151	127	249	953	4	2	3	
<i>Elliptio icterina</i>						1	3									1									
<i>Lasmigona subviridis</i>																						1	1		
<i>Pleurobema collina</i>														7		1	1	3			1				
<i>Strophitus undulatus</i>		2																							
<i>Villosa constricta</i>													6	11			1		5	3	5	5			
Total Taxa		2	1	1	0	2	2	0	0	0	0	0	2	3	1	3	3	2	2	2	3	3	2	1	
Total Mussels		304	145	302	0	235	848	0	0	0	0	0	985	591	152	66	91	154	132	252	959	10	3	3	
Mean Diversity (H')		0.02	0.00	0.00	0.00	0.01	0.02	0.00	0.00	0.00	0.00	0.00	0.02	0.10	0.00	0.06	0.03	0.04	0.07	0.04	0.04	0.04	0.05	0.00	
Mean Diversity (1-D)		0.01	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.01	0.06	0.00	0.06	0.04	0.04	0.07	0.02	0.01	0.64	0.67	0.00	
Total Search Effort (hrs)		7.47	4.97	7.02	4.88	5.22	10.28	3.03	3.45	3.48	1.77	2.20	2.43	17.80	19.70	8.67	15.90	14.50	13.10	12.70	10.00	16.20	12.22	12.50	
Mean CPUE		39.27	26.64	40.59	0.00	53.07	76.71	0.00	0.00	0.00	0.00	0.00	47.20	26.73	15.80	3.93	6.10	12.20	9.79	23.30	50.00	0.76	0.30	0.27	
Mean G-Rank		5.00	5.00	5.00	0.00	5.00	5.00	0.00	0.00	0.00	0.00	0.00	4.00	3.00	5.00	3.67	3.00	3.00	4.00	4.00	3.00	3.67	4.00	5.00	
Mean S-Rank		3.00	4.00	4.00	0.00	4.00	4.00	0.00	0.00	0.00	0.00	0.00	3.50	2.67	4.00	3.00	2.67	2.50	3.50	3.50	2.67	2.67	2.50	4.00	

Table 4. Mussel assemblage metrics from sites within the Tar River Drainage. I = intact dam, B = breached dam, R = relic dam. US = upstream reach, Mill = Mill reach, DS = downstream reach of the dam.

Mussel Taxa	Dam Stream Reach	Gooch's Mill (I) Tar River			Day's Mill (B) Tar River			Oxford City Dam (B) Tar River			Webb's Mill (B) Tar River			Camady's Mill (R) Tar River		
		US	Mill	DS	US	Mill	DS	US	Mill	DS	US	Mill	DS	US	Mill	DS
<i>Alasmidonta undulata</i>							2					1	1			
<i>Elliptio cistellaformis</i>								1		4		3	3	6	4	2
<i>Elliptio complanata</i>		1752	1307	765	102	64	3816	184	241	528	91	2020	4045	771	133	198
<i>Elliptio congaraea</i>							5									
<i>Elliptio fisheriana</i>				1							2	5	12			
<i>Elliptio icterina</i>		28	12	15				4	1	2	3	30	480	3		
<i>Elliptio lanceolata</i>														1		
<i>Elliptio mediocris</i>			13	2					2	1				1		1
<i>Elliptio roanokensis</i>															1	16
<i>Elliptio sp.</i>					5		4									
<i>Fusconaia masoni</i>		7					4					1	4			
<i>Lampsilis cariosa</i>									2	5		1	4	3		2
<i>Lampsilis n.s.</i>		37								1						
<i>Lampsilis radiata</i>			1		4		38									
<i>Lasmigona subviridis</i>								1					3			
<i>Pyganodon cataraeta</i>							7	2	2	4						
<i>Strophitus undulatus</i>			1									1	1			
<i>Villosa constricta</i>		3					2						2			
Total Taxa		5	5	4	3	1	8	5	5	7	3	8	10	6	3	5
Total Mussels		1827	1334	783	111	64	3878	192	248	545	96	2062	4555	785	138	219
Mean Diversity (H')		0.680	0.530	0.518	0.108	0	0.098	0.118	0.077	0.129	0.120	0.091	0.371	0.105	0.105	0.215
Mean Diversity (1-D)		0.080	0.040	0.045	0.154	0	0.032	0.081	0.056	0.061	0.101	0.040	0.200	0.035	0.071	0.178
Total Search Effort (hrs)		10.19	10.13	7.04	8.55	13.35	13.41	6.28	5.05	6.62	3.50	12.40	11.73	15.25	13.40	17.70
Mean CPUE		159.68	128.40	147.18	10.89	3.73	290.80	33.64	50.05	86.78	27.22	143.28	346.95	53.62	10.19	11.20
Mean G-Rank		3.67	5.00	4.67	5.00	5.00	3.86	4.50	4.40	4.14	4.50	4.00	3.80	3.67	4.00	3.75
Mean S-Rank		2.60	2.75	2.75	2.50	4.00	2.71	3.50	3.50	3.00	3.67	2.43	2.33	2.50	2.50	2.00

Table 4. (continued).

Mussel Taxa	Dam Stream Reach	Bellamy's Mill (I) Fishing Creek			Hamme's Mill (I) Fishing Creek			Powell's Mill (R) Fishing Creek			Laurel Mill (I) Sandy Creek		
		US	Mill	DS	US	Mill	DS	US	Mill	DS	US	Mill	DS
<i>Alasmidonta undulata</i>			3										
<i>Elliptio complanata</i>		610	3815	1992	72	4685	1234	293	224	390	595	892	205
<i>Elliptio congraeraea</i>				9		20	7		3		41	3	1
<i>Elliptio fisheriana</i>		1	41		3	7	9			2			
<i>Elliptio icterina</i>		13	50	178		129	91		19	32	30	19	5
<i>Elliptio lanceolata</i>							5	1	1	2			
<i>Elliptio mediocris</i>		890	2304	56		92	75						
<i>Elliptio roanokensis</i>			3593	113		146	15			2		5	
<i>Fusconaia masoni</i>		4					1				1	1	
<i>Lampsilis cariosa</i>		10	2										
<i>Lampsilis radiata</i>			17			2						1	
<i>Pyganodon cataracta</i>			2										
<i>Villosa constricta</i>											1	1	
Total Taxa		6	9	5	2	7	8	2	4	5	5	7	3
Total Mussels		1528	9827	2348	75	5081	1437	294	247	428	668	922	211
Mean Diversity (H')		0.852	0.454	0.681	0.105	0.578	0.826	0.037	0.204	0.170	0.234	0.520	0.086
Mean Diversity (1-D)		0.502	0.661	0.272	0.078	0.145	0.256	0.007	0.172	0.142	0.203	0.064	0.056
Total Search Effort (hrs)		16.51	23.38	13.98	8.47	16.28	12.64	7.68	5.13	8.34	12.55	9.48	9.69
Mean CPUE		104.45	385.84	171.52	8.83	299.54	114.65	32.72	55.39	51.70	52.35	98.36	21.54
Mean G-Rank		3.83	4.22	4.00	5.00	4.17	3.38	3.33	3.60	3.67	3.60	3.71	4.33
Mean S-Rank		2.60	2.63	3.00	3.50	5.00	2.43	2.50	3.00	2.60	3.00	2.43	3.67

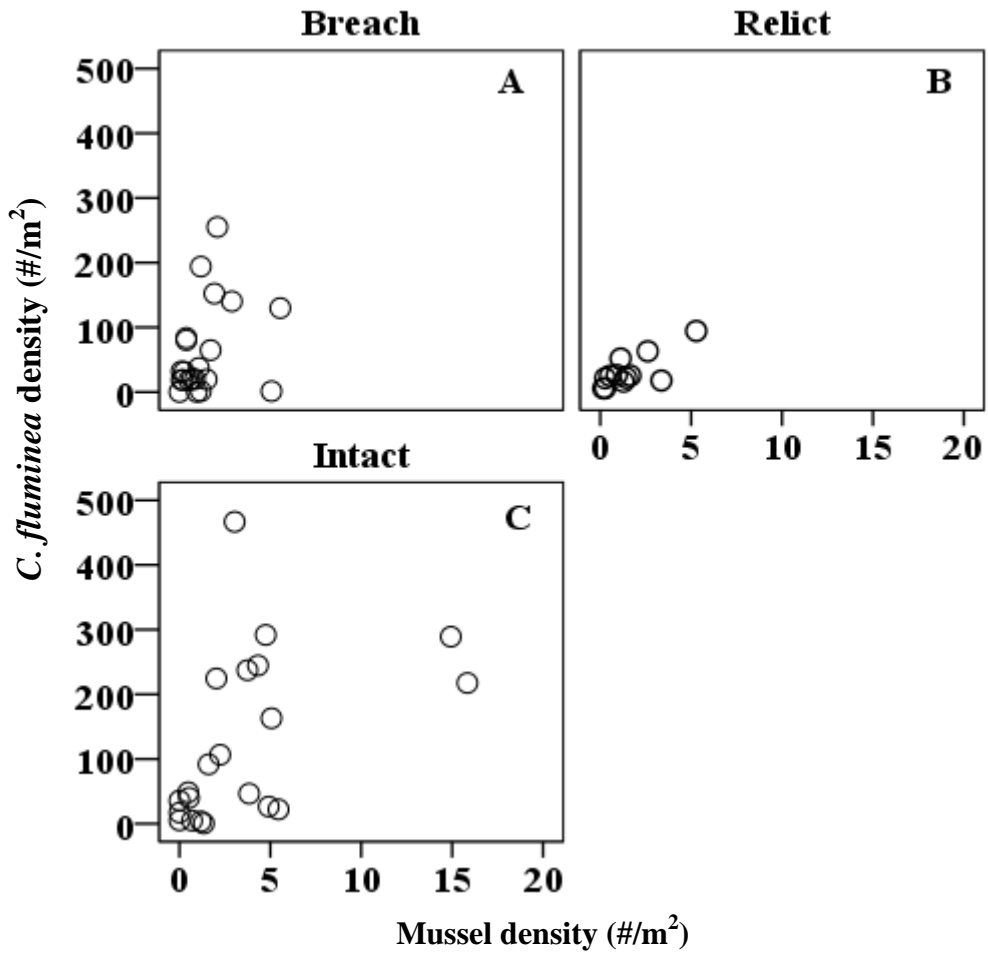


Figure 2. Relationships between freshwater mussel and *Corbicula fluminea* density (#/m²) for streams with breached (A, $r_s = 0.409$, $p = 0.065$), relict (B, $r_s = 0.585$, $p = 0.046$), and intact dams (C, $r_s = 0.541$, $p = 0.011$) in east-central North Carolina.

Table 5. GLM results for bivalve assemblage metric data. D = drainage, S = dam status, R = reach. * indicates interaction between factors. CPUE = catch-per-unit-effort. Significant effects are in bold.

Source of variation	Total mussels			Mean mussel density (#/m ²)			Total <i>C. fluminea</i>			Mean <i>C. fluminea</i> density (#/m ²)		
	df	F	<i>p</i>	df	F	<i>p</i>	df	F	<i>p</i>	df	F	<i>p</i>
Corrected Model	26	1.895	0.038	23	2.004	0.037	23	0.914	0.583	23	0.922	0.574
Intercept	1	117.634	0.000	1	316.504	0.000	1	65.783	0.000	1	71.087	0.000
D	2	5.006	0.012	2	4.370	0.022	2	3.675	0.037	2	3.738	0.036
S	2	0.869	0.428	2	1.841	0.176	2	3.017	0.064	2	3.130	0.058
R	2	1.135	0.333	2	0.539	0.589	2	0.911	0.413	2	0.892	0.421
D * S	4	1.878	0.135	3	2.633	0.068	3	0.250	0.861	3	0.248	0.862
D * R	4	0.293	0.880	4	0.441	0.778	4	0.031	0.998	4	0.034	0.998
S * R	4	1.370	0.263	4	1.015	0.415	4	0.604	0.662	4	0.609	0.659
D * S * R	8	1.192	0.331	6	1.067	0.404	6	0.149	0.988	6	0.141	0.990
Error	36			30			30			30		
Total	63			54			54			54		
Corrected Total	62			53			53			53		

Source of variation	Mean mussel CPUE			Mussel H'			Simpson's Index			Total mussel richness		
	df	F	<i>p</i>	df	F	<i>p</i>	df	F	<i>p</i>	df	F	<i>p</i>
Corrected Model	26	2.686	0.003	26	6.331	0.000	26	2.965	0.001	26	3.565	0.000
Intercept	1	233.820	0.000	1	15570.343	0.000	1	13531.547	0.000	1	2326.859	0.000
D	2	9.057	0.001	2	56.799	< 0.001	2	26.452	< 0.001	2	28.251	< 0.001
S	2	0.560	0.576	2	11.478	< 0.001	2	5.305	0.010	2	2.307	0.114
R	2	2.041	0.145	2	0.136	0.874	2	0.530	0.593	2	0.750	0.480
D * S	4	3.476	0.017	4	3.578	0.015	4	1.410	0.250	4	1.762	0.158
D * R	4	0.400	0.807	4	0.407	0.802	4	0.459	0.765	4	1.412	0.250
S * R	4	1.151	0.348	4	0.281	0.888	4	0.736	0.573	4	1.202	0.327
D * S * R	8	1.578	0.166	8	0.400	0.913	8	0.458	0.877	8	0.731	0.663
Error	36			36			36			36		
Total	63			63			63			63		
Corrected Total	62			62			62			62		

Table 6. GLM results for response ratios with a significant dam status effect within drainage.

US = upstream, M = mill, DS = downstream reach. Significant results are in bold.

Response Ratio Drainage	Mean Total Mussel (M/DS)								
	Neuse			Roanoke			Tar		
Source of variation	df	F	<i>p</i>	df	F	<i>p</i>	df	F	<i>p</i>
Corrected Model	2	2.954	0.195	2	3.923	0.145	2	6.217	0.034
Intercept	1	0.293	0.626	1	2.303	0.226	1	1.051	0.345
Status	2	2.954	0.195	2	3.923	0.145	2	6.217	0.034
Error	3			3			6		
Total	6			6			9		
Corrected Total	5			5			8		

Response Ratio Drainage	Mussel Density (M/DS)								
	Neuse			Roanoke			Tar		
Source of variation	df	F	<i>p</i>	df	F	<i>p</i>	df	F	<i>p</i>
Corrected Model	2	1.757	0.313	--	--	--	2	37.786	0.000
Intercept	1	1.803	0.272				1	0.030	0.869
Status	2	1.757	0.313				2	37.786	0.000
Error	3						6		
Total	6						9		
Corrected Total	5						8		

Response Ratio Drainage	Mussel CPUE (M/DS)								
	Neuse			Roanoke			Tar		
Source of variation	df	F	<i>p</i>	df	F	<i>p</i>	df	F	<i>p</i>
Corrected Model	2	2.583	0.223	2	19.046	0.020	2	3.745	0.088
Intercept	1	1.723	0.281	1	14.292	0.032	1	0.716	0.430
Status	2	2.583	0.223	2	19.046	0.020	2	3.745	0.088
Error	3			3			6		
Total	6			6			9		
Corrected Total	5			5			8		

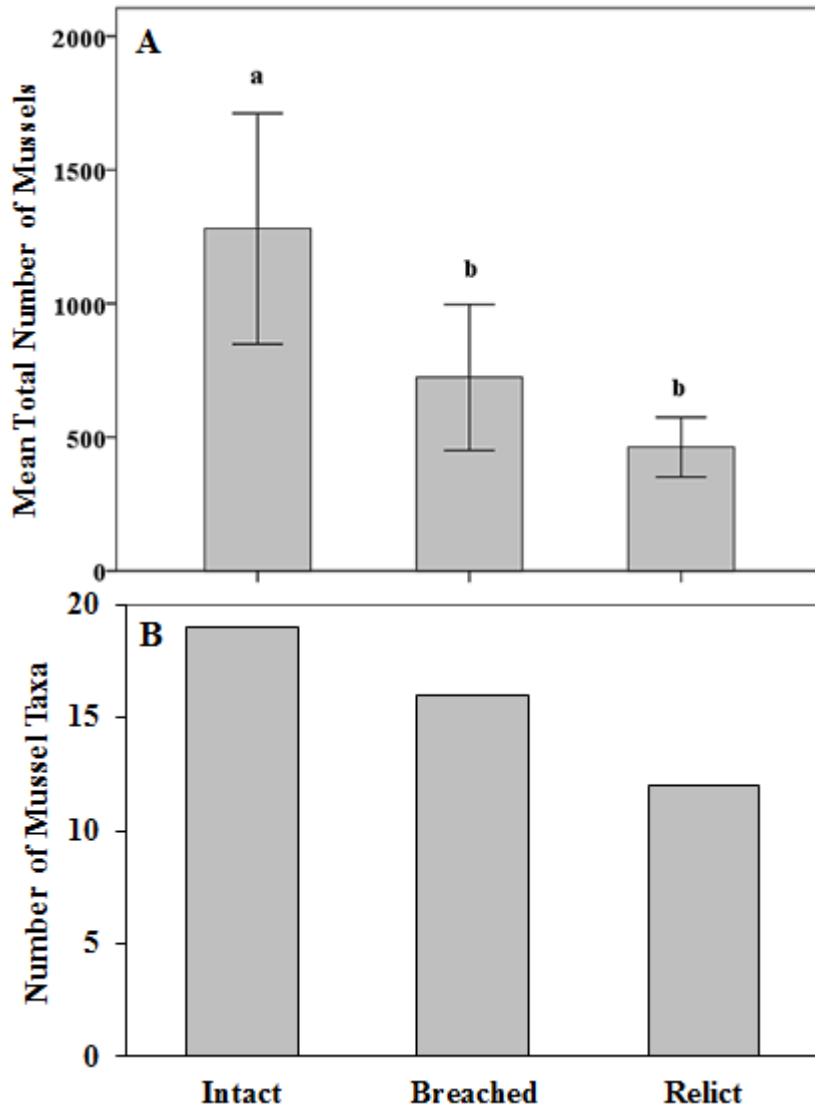


Figure 3. Mean (\pm 1SE) total number of freshwater mussels (A) and taxa (B) encountered alive in streams with intact, breached, or relict dams in east-central North Carolina. Bars sharing the same letter are not significantly different from one another (LSD post-hoc, $p > 0.05$).

Table 7. Means (+/-SE) for bivalve assemblage parameters for each reach within a given dam type. I = intact, B = breached, R = relict dam. US = upstream reach, Mill = mill reach, DS = downstream reach. CPUE = catch-per-unit-effort.

Parameter	Status	Reach	Mean+/-SE	N	Parameter	Status	Reach	Mean+/-SE	N
Total Mussels	I	US	43.60 (4.87)	135	Mussel H'	I	US	0.41 (0.03)	135
		Mill	154.03 (22.29)	135			Mill	0.43 (0.03)	135
		DS	79.63 (10.37)	135			DS	0.45 (0.03)	135
	B	US	9.71 (1.50)	90		B	US	0.22 (0.04)	90
		Mill	17.63 (2.87)	90			Mill	0.22 (0.04)	90
		DS	21.9 (3.07)	90			DS	0.18 (0.32)	90
	R	US	19.09 (2.25)	119		R	US	0.18 (0.02)	119
		Mill	16.57 (3.47)	120			Mill	0.12 (0.02)	120
		DS	68.26 (9.16)	119			DS	0.21 (0.03)	119
Mussel CPUE (#/hr)	I	US	52.25 (4.88)	135	Richness	I	US	2.11 (0.12)	135
		Mill	127.54 (13.67)	135			Mill	2.97 (0.17)	135
		DS	106.07 (11.64)	135			DS	2.53 (0.15)	135
	B	US	18.76 (2.57)	90		B	US	1.17 (0.12)	90
		Mill	31.63 (5.26)	90			Mill	1.34 (0.12)	90
		DS	38.34 (5.14)	90			DS	1.27 (0.10)	90
	R	US	24.68 (2.58)	119		R	US	1.34 (0.08)	119
		Mill	24.41 (4.66)	120			Mill	1.15 (0.09)	120
		DS	78.78 (10.09)	119			DS	1.88 (0.12)	119
Mussel Density (#/m ²)	I	US	2.10 (0.29)	120	<i>C. fluminea</i> Density (#/m ²)	I	US	66.07 (9.55)	120
		Mill	5.76 (0.70)	120			Mill	194.91 (17.47)	120
		DS	2.57 (0.32)	120			DS	101.24 (12.22)	120
	B	US	0.41 (0.09)	90		B	US	53.48 (8.50)	90
		Mill	0.85 (0.19)	90			Mill	74.59 (13.83)	90
		DS	1.04 (0.18)	90			DS	42.12 (6.72)	90
	R	US	1.24 (0.18)	90		R	US	21.59 (2.20)	90
		Mill	0.80 (0.21)	90			Mill	19.46 (3.39)	90
		DS	2.20 (0.35)	90			DS	27.31 (3.96)	90

Table 8. Mixed models analysis for testing effect of reach on bivalve assemblage parameters within a given dam type. Mill = mill reach, DS = downstream reach. Degrees of freedom are reported as numerator, denominator df. Stream(Drainage) added as a random effect. Upstream reach is the reference and set to 0.

Parameter	Status	Reach	df	Estimate (SE)	F	p
Total Mussels	Intact	Mill	2, 396	110.43 (18.09)	19.38	< 0.001
		DS		36.03 (18.09)		
	Breached	Mill	2, 262	7.922 (3.45)	6.481	0.002
		DS		12.23 (3.45)		
	Relict	Mill	2, 351	-2.40 (7.76)	28.36	< 0.001
		DS		49.43 (7.77)		
Mussel CPUE (#/hr)	Intact	Mill	2, 396	75.29 (12.73)	18.56	< 0.001
		DS		53.81 (12.73)		
	Breached	Mill	2, 262	12.87 (5.81)	5.87	0.003
		DS		19.58 (5.81)		
	Relict	Mill	2, 351	-0.08 (8.76)	25.85	< 0.001
		DS		54.49 (8.76)		
Mussel H'	Intact	Mill	2, 396	0.02 (0.03)	0.80	0.451
		DS		0.04 (0.03)		
	Breached	Mill	2, 262	-0.000168 (0.03)	1.00	0.370
		DS		-0.04 (0.03)		
	Relict	Mill	2, 351	-0.06 (0.03)	5.68	0.004
		DS		0.03 (0.03)		
Richness	Intact	Mill	2, 396	0.86 (0.16)	15.10	< 0.001
		DS		0.42 (0.16)		
	Breached	Mill	2, 262	0.18 (0.11)	1.26	0.280
		DS		0.10 (0.11)		
	Relict	Mill	2, 351	-0.19 (0.10)	29.01	< 0.001
		DS		0.55 (0.10)		
Mussel Density (#/m ²)	Intact	Mill	2, 352	3.67 (0.62)	20.73	< 0.001
		DS		0.47 (0.62)		
	Breached	Mill	2, 262	0.44 (0.20)	5.17	0.006
		DS		0.63 (0.20)		
	Relict	Mill	2, 264	-0.44 (0.35)	8.57	< 0.001
		DS		0.96 (0.35)		
<i>C. fluminea</i> Density (#/m ²)	Intact	Mill	2, 352	128.84 (15.27)	38.05	< 0.001
		DS		35.17 (15.27)		
	Breached	Mill	2, 262	21.10 (10.60)	4.83	0.009
		DS		-11.37 (10.60)		
	Relict	Mill	2, 264	-2.13 (3.86)	2.21	0.112
		DS		5.72 (3.86)		

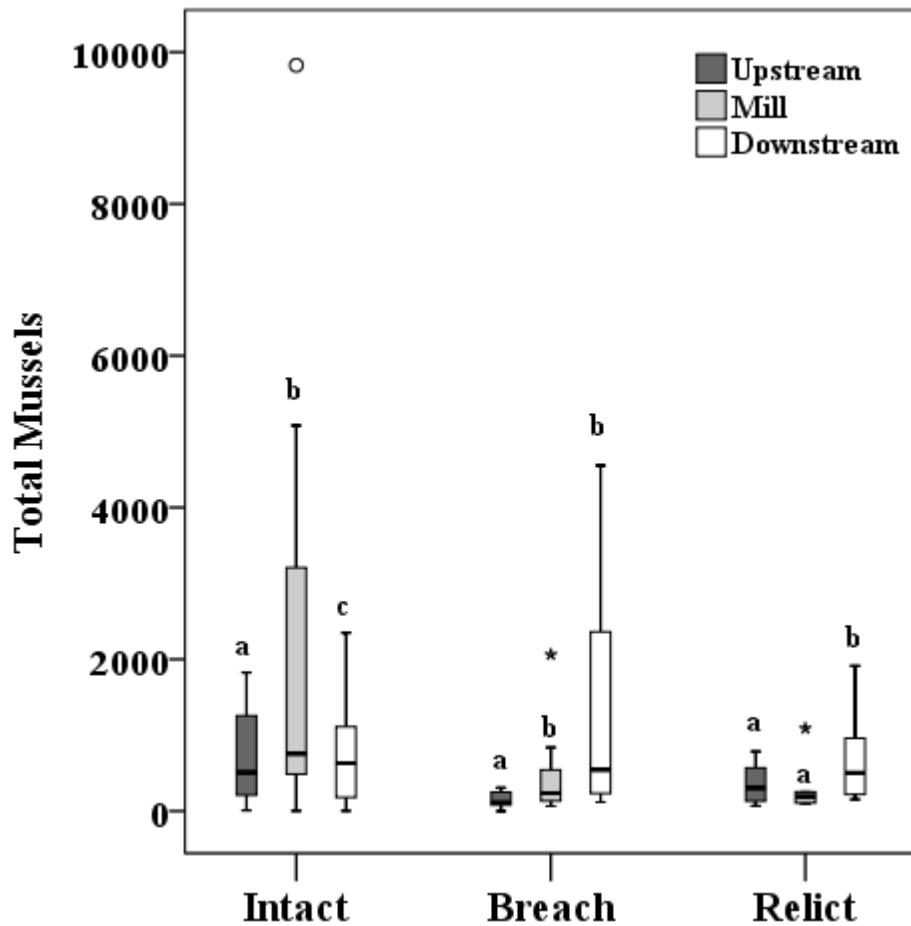


Figure 4. Box plots of freshwater mussel abundance at sites located upstream, immediately downstream (Mill) and >500 m downstream of breached, intact and relict dams in east-central North Carolina. The center line represents the median, the box upper and lower bounds the 25th and 75th percentiles of the data. The open circle represents a value that is 1.5 or 3 times the interquartile range and the asterisks denote values that are more than 3 times the interquartile range. Box plots sharing the same letter are not statistically different from each other within a given dam type (LSD post-hoc, $p > 0.05$).

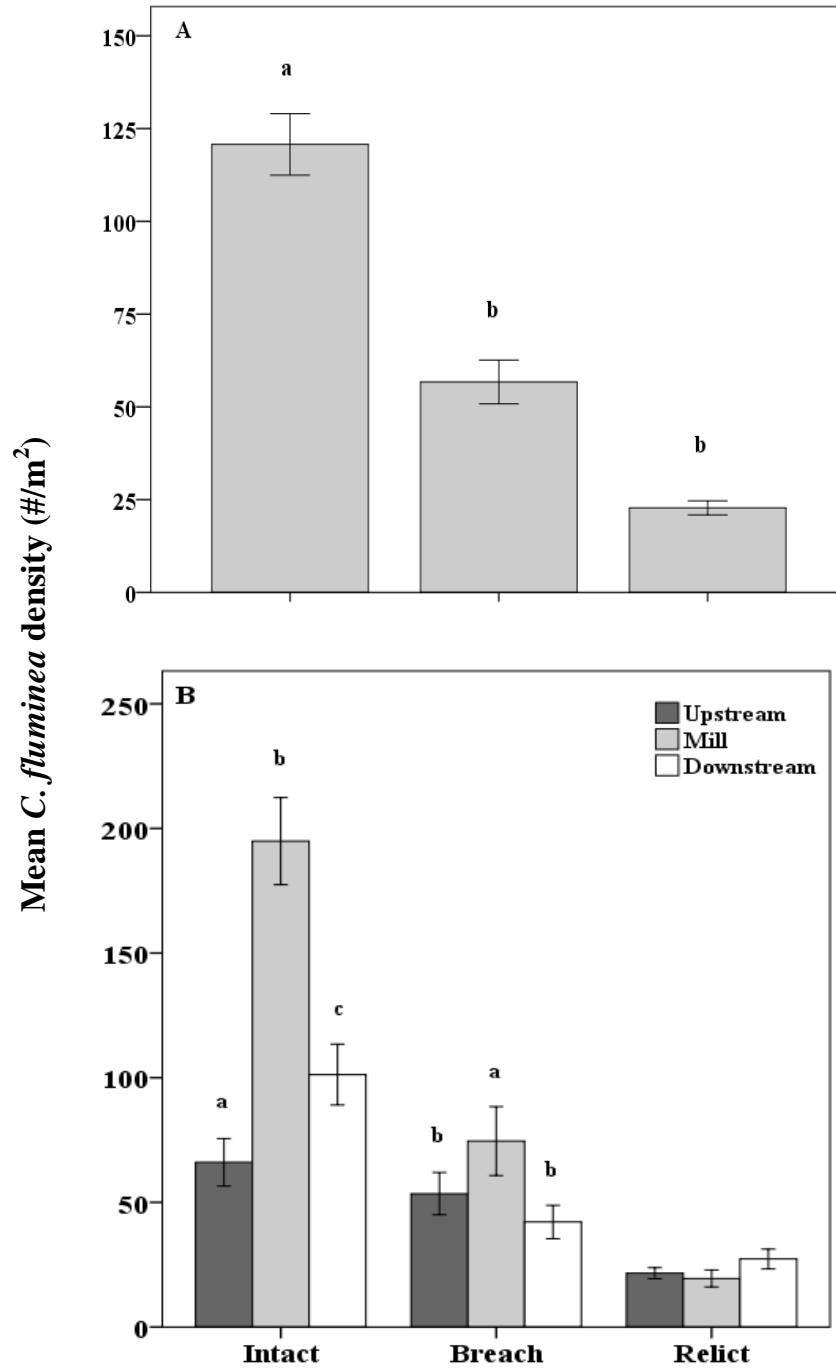


Figure 5. Mean *Corbicula fluminea* densities (#/m², +/- 1 SE) in streams with intact, breached, or relict small dams (A) and at sites located upstream, immediately downstream (Mill) and >500 m downstream from dams (B) in east-central North Carolina. Bars sharing the same letter are not significantly different from each other (post-hoc, $p > 0.05$).

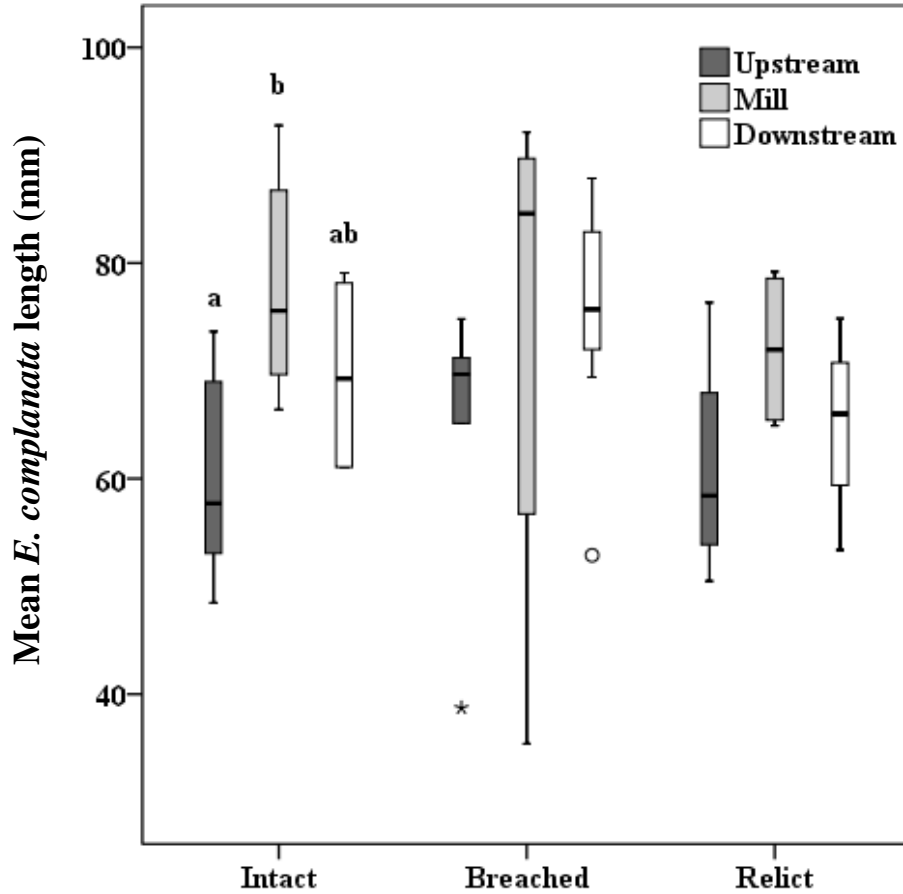


Figure 6. Box plots of mean *Elliptio complanata* length at sites located upstream, immediately downstream (Mill) and >500 m downstream of intact, breached and relict dams in east-central North Carolina. The center line represents the median, the box upper and lower bounds the 25th and 75th percentiles of the data. The open circle represents a value that is 1.5 or 3 times the interquartile range and the asterisk denotes a value that is more than 3 times the interquartile range. Different letters denote significant differences between reaches of a given dam type (Tukey HSD post-hoc, $p < 0.05$). There were no significant differences between dam types (ANOVA, $p > 0.05$).

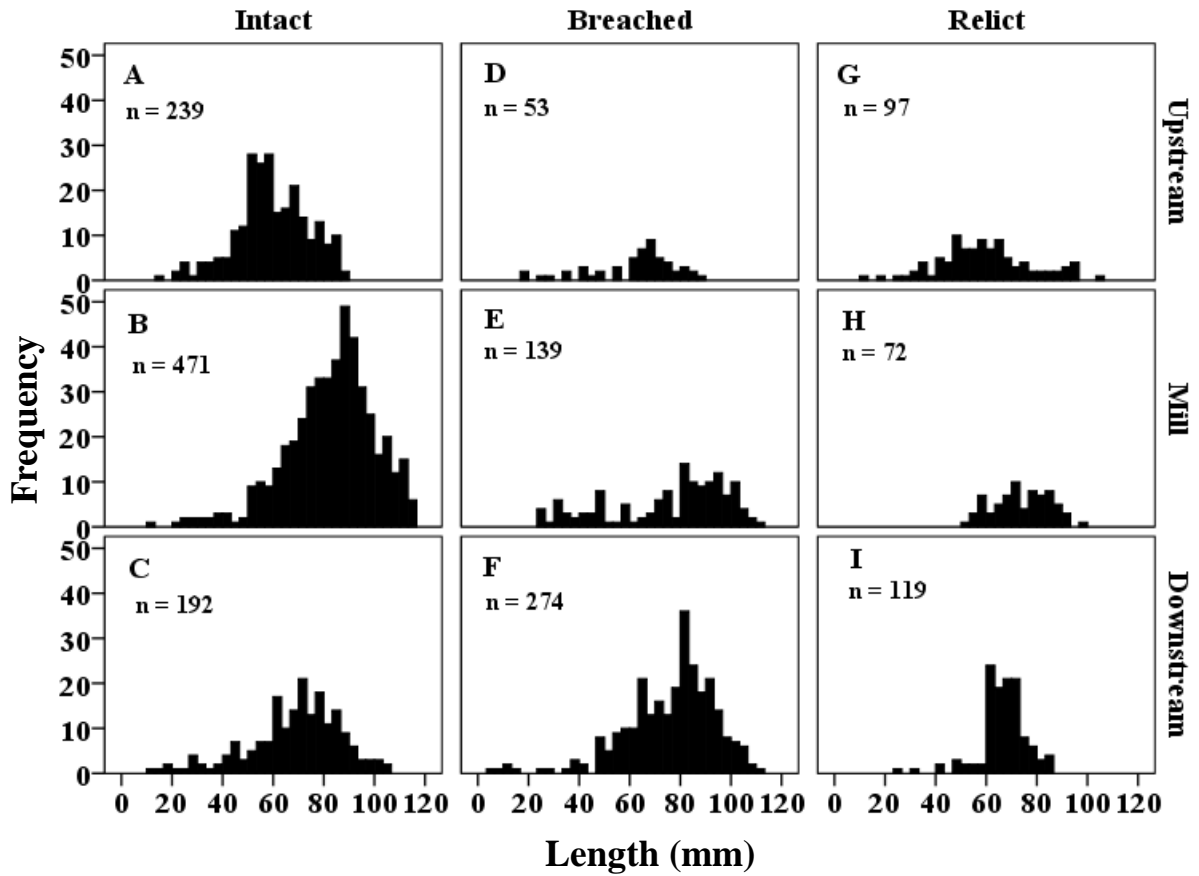


Figure 7. Length-frequencies of *Elliptio complanata* ($n = 1,656$) collected from quadrats at sites located upstream (A, D, G), in the mill reach (B, E, H) and >500 m downstream (C, F, I) from 6 intact, 7 breached and 4 relict dams in east-central North Carolina.

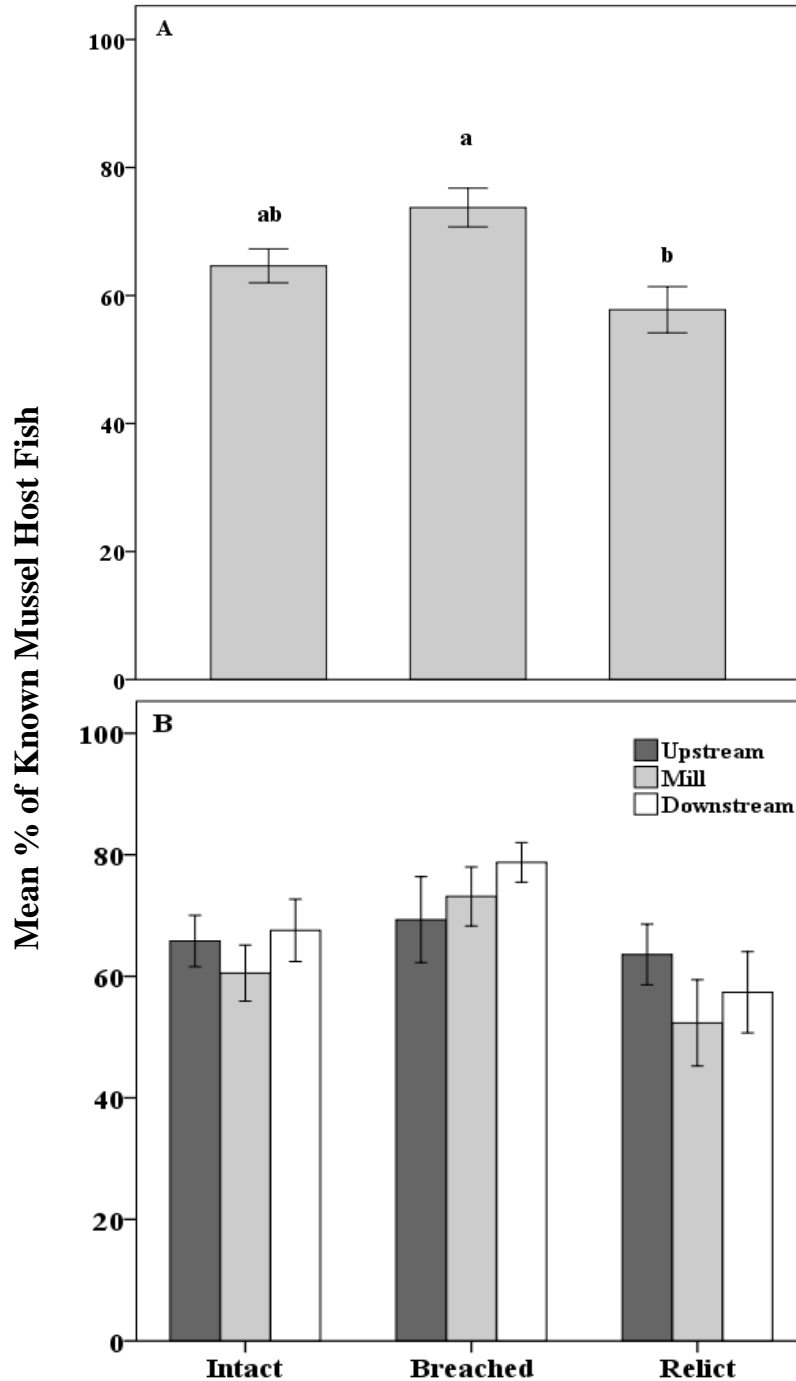


Figure 8. The mean % of known mussel host-fish (+/- 1 SE) in streams with intact, breached or relict dams (A) and at sites located upstream, immediately downstream (Mill) and >500 m downstream from dams (B) in east-central North Carolina. Different letters denote significant differences between dam types ($p < 0.05$). There were no significant between-reach differences within dam types ($p > 0.05$).

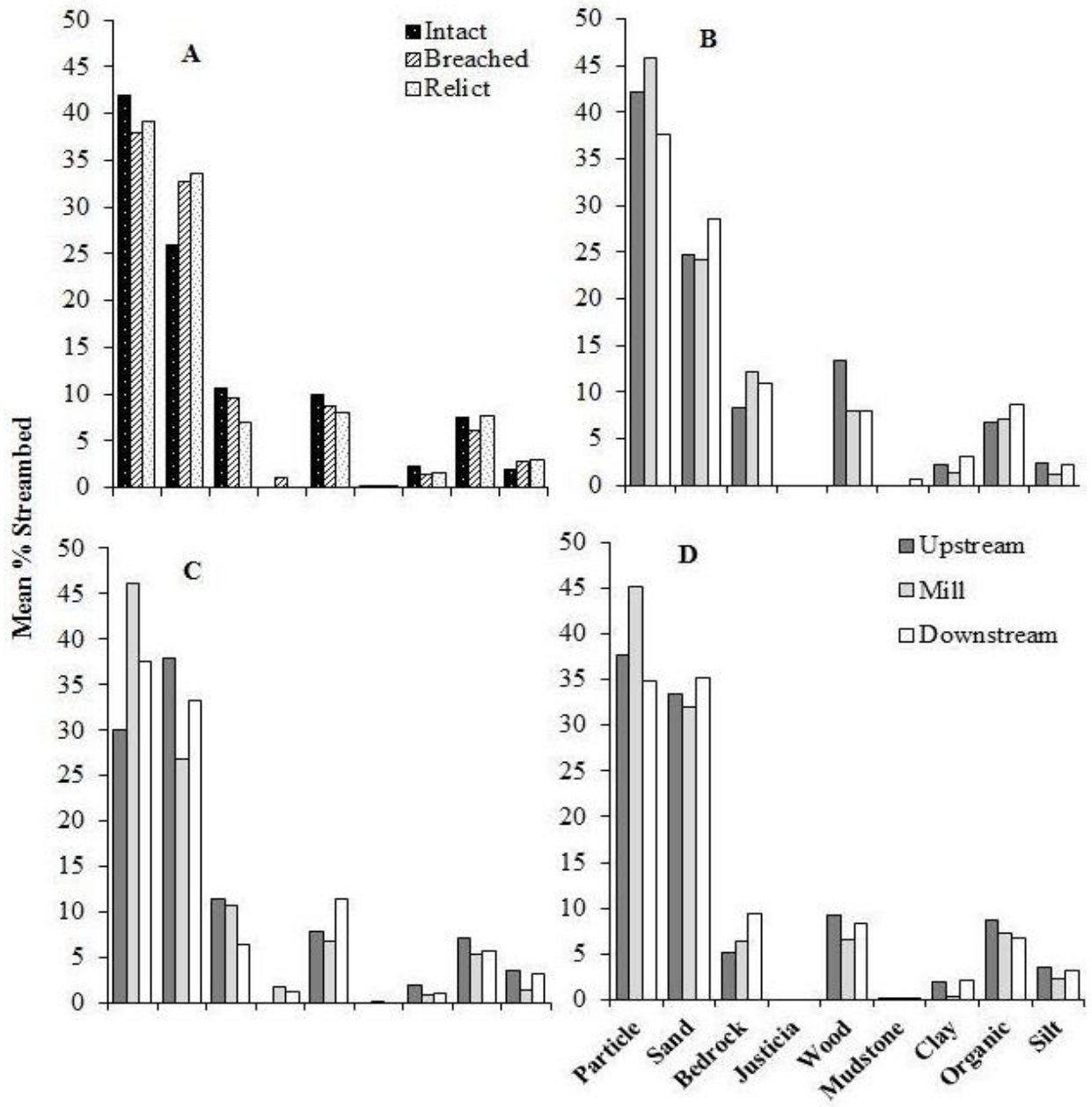


Figure 9. Mean percentage of physical streambed habitat comprised of 9 substrate categories at all dam types (A) and at sites located upstream, immediately downstream (Mill) and > 500 m downstream of 8 intact (B), 8 breached (C) and 7 relict dams (D) in east-central North Carolina. Particle = cobble/gravel substrate.

Table 9. Mean percentages of streambed habitat comprised of 9 substrate categories at sites located upstream, immediately downstream (Mill) and downstream > 500 m from 8 intact, 8 breached and 7 relict dams in east-central North Carolina. All = means of all reaches together within each dam type.

Status	Reach	Gravel	Sand	Bedrock	<i>Justicia</i>	Wood	Mudstone	Clay	Organic	Silt
Intact	All	41.92	25.84	10.52	0.00	9.87	0.22	2.20	7.54	1.89
	US	42.15	24.75	8.40	0.00	13.47	0.00	2.15	6.76	2.32
	Mill	45.89	24.22	12.17	0.00	8.07	0.00	1.31	7.18	1.17
	DS	37.72	28.54	11.00	0.00	8.06	0.67	3.16	8.67	2.20
Breached	All	37.88	32.68	9.50	1.03	8.65	0.06	1.33	6.10	2.78
	US	30.04	37.87	11.40	0.00	7.81	0.00	2.01	7.21	3.65
	Mill	46.06	26.87	10.68	1.84	6.74	0.17	0.86	5.32	1.47
	DS	37.53	33.31	6.43	1.24	11.40	0.00	1.11	5.77	3.22
Relict	All	39.21	33.52	6.95	0.00	8.08	0.12	1.48	7.58	3.06
	US	37.63	33.42	5.15	0.00	9.29	0.23	2.03	8.74	3.51
	Mill	45.22	31.93	6.36	0.00	6.53	0.01	0.29	7.27	2.38
	DS	34.78	35.22	9.33	0.00	8.41	0.13	2.12	6.74	3.28

Table 10. Statistically significant ($p < 0.05$) Spearman correlation coefficients for associations between mussel assemblages and stream physical habitat parameters from sites in the Neuse, Roanoke and Tar River drainages from 2009-2011. Channel width, depth, percent silt, percent mudstone, and median particle size are excluded from the table because there were not any statistically significant associations with mussel parameters. Missing data (---) indicate non-significant correlations.

Habitat Parameter	Total Mussels	Mean Mussels	Mean Mussel CPUE	Mussel H'	Mean Mussel Richness
\bar{x} Velocity (m/s)	---	---	$r_s = -0.276$ $p = 0.029$ $n = 63$	---	---
\bar{x} Particle Size (mm)	---	---	---	$r_s = -0.293$ $p = 0.021$ $n = 62$	$r_s = -0.253$ $p = 0.047$ $n = 62$
% Clay	$r_s = 0.279$ $p = 0.027$ $n = 63$	---	$r_s = 0.366$ $p = 0.003$ $n = 63$	$r_s = 0.365$ $p = 0.003$ $n = 63$	$r_s = 0.302$ $p = 0.016$ $n = 63$
% Sand	---	---	$r_s = 0.266$ $p = 0.035$ $n = 63$	---	---
% Organic	---	---	---	$r_s = 0.284$ $p = 0.024$ $n = 63$	---
% Wood	---	---	$r_s = 0.321$ $p = 0.01$ $n = 63$	$r_s = 0.315$ $p = 0.012$ $n = 63$	$r_s = 0.277$ $p = 0.028$ $n = 63$
% Bedrock	---	$r_s = -0.272$ $p = 0.031$ $n = 63$	$r_s = -0.295$ $p = 0.019$ $n = 63$	---	---

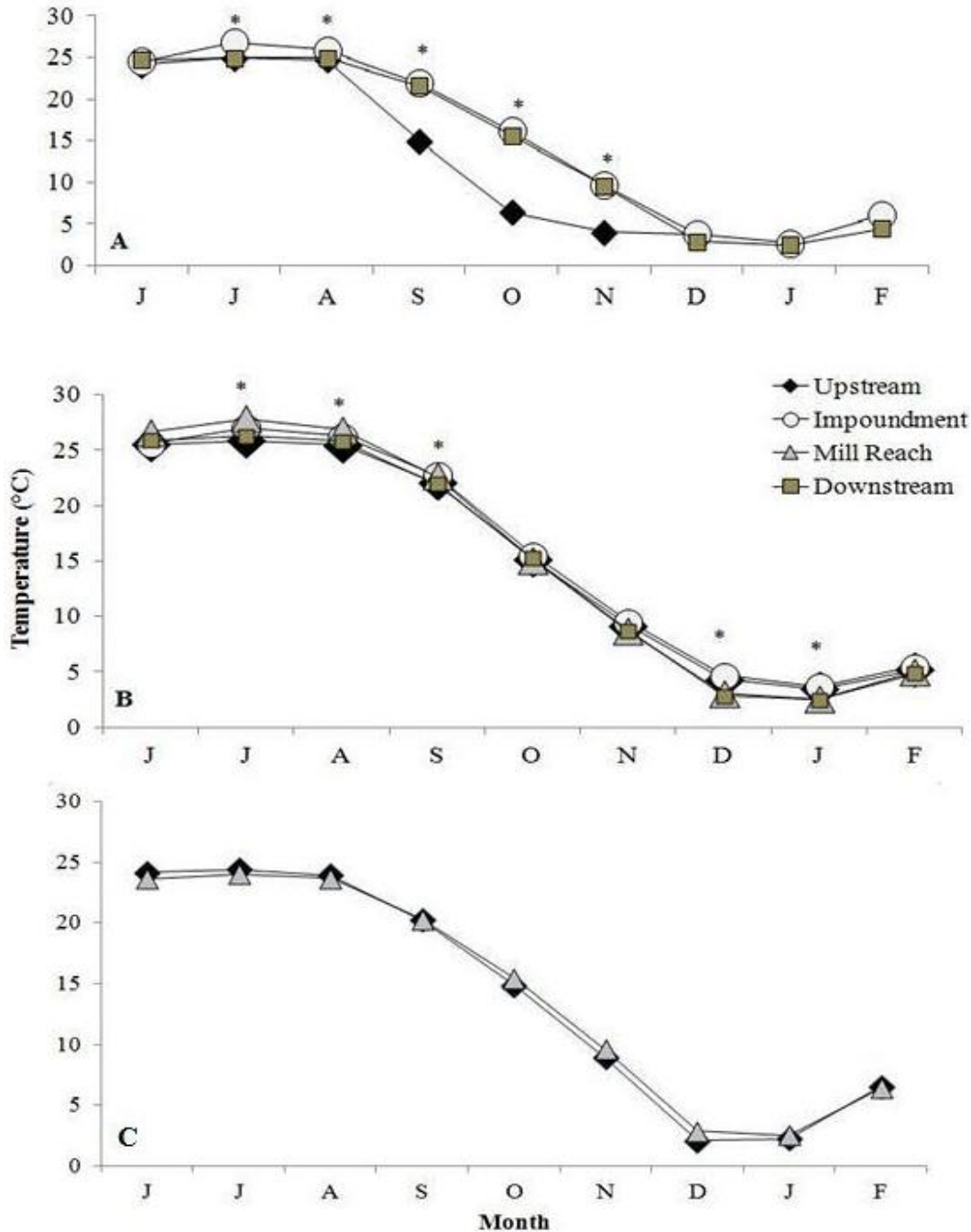


Figure 10. Temperature means from the Tar River drainage during months of June 2010-February 2011 at sites located upstream, within the impoundment, immediately below (mill reach) and downstream >500 m from intact Gooch's Mill (A), breached Oxford City (B) and relict Powell's Mill (C) dam. Asterisks indicate significant temperature differences between reaches (Tukey HSD, $p < 0.05$). Powell's Mill downstream logger was lost.

Table 11. Statistically significant (***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$) Spearman correlation coefficients between mussel assemblage and land use parameters at 57 sites and sites associated with 12 Piedmont and 8 Coastal Plain dams in Neuse, Roanoke and Tar River drainages. Open water and barren land were excluded from analyses (surface cover $< 1\%$). Rank and link magnitude and area were excluded from table due to non-significant correlations. Mussel Density and Total Site Richness were removed from Coastal Plain sites. Missing data (---) indicate non-significant correlations.

All Sites (n = 57)	Total Urban	Pasture	Crop	Deciduous Forest	Evergreen Forest	Mixed Forest	Wetland	Grass
Total Mussels	---	---	0.264*	---	0.272*	---	0.369**	---
Mussel CPUE	---	---	---	---	0.37**	0.297*	0.371***	0.296*
Mussel Density (n = 26)	---	---	---	---	---	---	0.500***	---
H'	0.472***	---	0.721***	-0.718***	0.373**	---	0.667***	0.376**
Total Site Richness	0.293*	---	0.539***	-0.458***	0.436***	---	0.513***	0.376**
Piedmont (n = 35)								
Total Mussels	---	---	0.401*	---	---	---	0.482**	---
\bar{x} Mussel CPUE	---	---	0.433**	-0.346*	---	---	0.515**	0.396**
Mussel Density (n = 26)	---	---	---	---	---	---	0.589**	---
H'	0.461**	0.455**	0.729***	-0.775***	0.371*	0.447**	0.735***	0.708***
Total Site Richness	---	0.359*	0.557***	-0.629***	0.421**	---	0.565***	0.748***
Coastal Plain (n = 22)								
Total Mussels	---	---	---	---	---	---	---	---
\bar{x} Mussel CPUE	---	---	---	0.506*	0.585**	---	---	---
H'	---	-0.640***	0.483*	---	---	-0.493*	0.519**	-0.505*
\bar{x} Mussel Richness	---	-0.502*	---	---	---	---	---	---

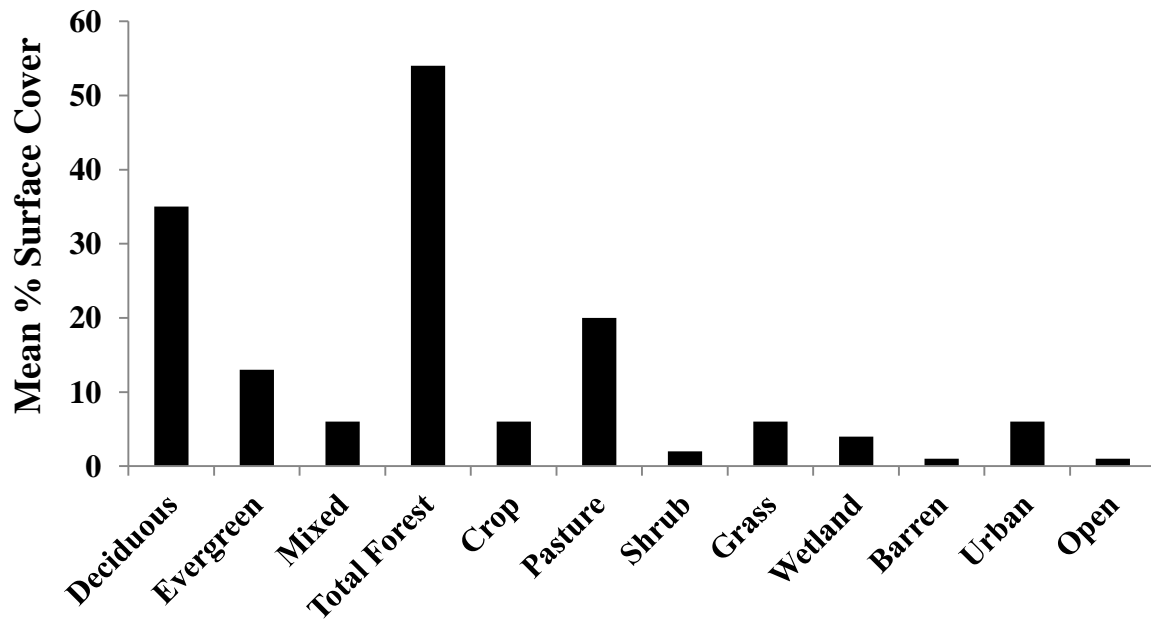


Figure 11. Mean percentage of land use surface cover at 57 sites associated with intact, breached and relict dams in east-central North Carolina. Total Forest comprises of deciduous, evergreen and mixed forest types.

BIOGRAPHICAL INFORMATION

Megan Anne McCormick was born in Rome, Georgia, in 1983. She attended elementary through high school in Rome and graduated from Armuchee High in 2002. Ms. McCormick enrolled at the College of Charleston, South Carolina, to study Marine Biology and was awarded a Bachelor of Science degree in December 2006. Through 2007 to the summer of 2009, Ms. McCormick enhanced her freshwater biology field techniques while working with the North Carolina Wildlife Resources Commission in Raleigh, North Carolina. In the fall of 2009, Ms. McCormick accepted a graduate assistantship with Dr. Michael Gangloff at Appalachian State University in Boone, North Carolina. The Master of Science degree in biology was awarded in May 2012. Ms. McCormick's parents are Christy Lynn and Dr. Jerry McCormick of Rome, Georgia.