THE EFFECTS OF BEAVER IMPOUNDMENTS ON MONTANE STREAM FISH
COMMUNITES

A Thesis by
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May 2020

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Abstract

THE EFFECTS OF BEAVER IMPOUNDMENTS ON MONTANE STREAM FISH
COMMUNITES

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North American beavers (*Castor canadensis*) are ecological engineers, and their dams alter

stream hydrology, sediment dynamics, nutrient cycling, riparian communities, and water

chemistry. Impacts of beaver dams on fish communities are complex and regionally-variable.

Few previous studies have examined the effect of beaver dams on the fishes of the Southern

Appalachians, likely because beaver populations in this region are still recovering from historical

over-exploitation. Populations in the Southern Appalachians have been increasing slightly, but

are still at relatively low levels. I sampled fish communities during the summer of 2019 from 9

streams with active beaver ponds and 7 with inactive beaver ponds. Four sites were sampled for

fishes in each stream and sediment cores were taken from all ponds in the study in order to

quantify the abundance of oligochaete worms, potential hosts for the myxozoan fish parasite

Myxobolus cerebralis. I found that both active and inactive beaver impoundments affect stream

physicochemical habitat parameters, fish community structure and possibly the potential for

disease transmission. Generalized linear mixed effect models (GLMMs) indicate that fish

diversity is reduced in streams with active beaver impoundments and that the magnitude of this

reduction is dependent on the proximity of a site relative to an active impoundment. Models

indicate that site elevation plays the strongest role in determining fish species richness. Further,

GLMMs indicate that beaver activity and proximity to a dam were important predictors of dissolved oxygen (DO) saturation and water temperature. Although active ponds had lower DO they also had slightly lower temperatures. Indicator species analysis found that two species had a significant association with active beaver ponds whereas 8 were associated with inactive beaver ponds or unimpounded reaches up and downstream from active beaver ponds. The probability of detecting oligochaetes and oligochaete density were greater in active compared to inactive beaver ponds. However, relatively few worms in the family Tubificidae were encountered and no abnormal salmonids were detected during fish surveys. My work indicates that Appalachian Mountain streams with active beaver ponds support less diverse fish assemblages than streams where beaver ponds have been abandoned. However, both *Semotilus atromaculatus* and *Salmo trutta* appear to prefer active beaver ponds. My results also indicate that beaver ponds may improve habitat for freshwater oligochaetes but the potential role of impoundments in fish disease transmission remains unclear.

important was the support of my parents, Frederick and Gayge Fritz, and that of my sister Anna

Fritz. Without their constant efforts to instill a love of the outdoors in me, and unrelenting

support for my goals and aspirations, none of this work would have ever come to fruition.

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Foreword

The research detailed in this thesis will be submitted to the peer-reviewed journal *Freshwater Biology*. This thesis has been formatted according to the style requirements for publication in this journal.

Introduction

North American beavers (*Castor canadensis*) are ecological engineers and their activities may substantially alter ecosystems through non-trophic effects (Jones et al. 1994, Schlosser and Kallemeyn 2000, Colleen and Gibson, 2001). Beaver dams form temporary lentic habitats within stream networks and alter hydrology, sediment dynamics, nutrient cycling, riparian communities, and water chemistry (Johnston and Naiman 1990, Gibson et al. 2014). The impact of beaver dams on fish communities is complex, and may both positively and negatively affect diversity (Snodgrass and Meffe 1998, Schlosser and Kallemeyn 2000, Colleen and Gibson 2001, Kemp et al 2011, Smith and Mather 2013). Much of the variability in responses to beaver impoundments is attributable to biogeographic and taxonomic variation in fish communities as well as pond morphology and successional stage (Schlosser and Kallemeyn 2000, Kemp et al. 2011, Smith and Mather 2013). Beavers have long been prized for their fur, and their populations were decimated by the North American fur trade. Native beavers were completely extirpated from North Carolina by 1897 and were not reintroduced to the state until 29 individuals were brought in from Pennsylvania in 1939 (McGrath et al. 2018). Since their reintroduction, beavers have become common throughout the state, including in the western region (McGrath et al. 2018). The return of these ecosystem engineers to the southern mountains raises questions about their impact on freshwater communities.

Although beaver impoundments affect fishes throughout their life cycle, body size and life history can have important implications for how taxa respond to dams. For example, Schlosser and Kallemeyn (2000) found that collapsed beaver dams on the Kabetogama Peninsula in Minnesota may provide habitat for juvenile fishes dispersing from an adjacent large lake. Sites that were closer to the lake also had higher species richness compared with those farther away

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(Schlosser and Kallemeyn 2000). Juveniles of species typically found only in nearby lakes were absent from ponds with intact dams, suggesting that collapsed ponds also provide important habitat for lentic species dispersing through lotic ecosystems, whereas intact dams may act as barriers to dispersal (Schlosser and Kalleymeyn 2000). Conversely, intact beaver impoundments in Oregon supported higher densities of juvenile steelhead (*Onchorynchus mykiss*) compared to unimpounded reaches in the same streams (Bouwes et al. 2016). Both adult and juvenile PIT tagged steelhead were frequently detected moving over intact beaver dams both upstream and downstream (Bouwes et al 2016). Although salmonids are adept at bypassing obstacles they were absent from the sites on the Kabetogama Peninsula where the majority of fishes observed were small-bodied taxa that were likely unable to move upstream of beaver dams (Schlosser and Kalleymeyn 2000).

Beaver activity may positively affect fish diversity by increasing the variability of aquatic habitats in a system. The depth, width, and temperature of beaver-impounded streams is much more variable than unimpounded systems, and these systems may provide habitats and trophic niches that may be absent or uncommon in unimpounded streams (Bouwes et al. 2016). Beaver ponds in Massachusetts were associated with increased diversity of native fish species, possibly due to increased habitat heterogeneity (Smith and Mather 2013). Beavers also introduce coarse woody debris (CWD) into streams during the construction and rebuilding of dams, and through the inundation and death of riparian woody plants due to rising water tables (Pollock et al. 1995). CWD provides shelter for juvenile and adult fishes and plays an important role in stream productivity in many regions (Kemp et al. 2011). Beaver-associated CWD may also provide habitat and food resources for invertebrates, increasing available forage for fish (Kemp et al. 2011, Smith and Mather 2013).

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In arid environments, beaver impoundments may improve water retention and fish habitat but this may also promote the establishment of invasive species. For example, beaver ponds on the Verde River in Arizona harbored a higher proportion of non-native fishes compared to unimpounded reaches (Gibson et al. 2014). In contrast, a study of 21 beaver dams in Northern Utah found that native *Oncorhynchus clarkii* were able to pass upstream of dams at a much higher rate than invasive *Salmo trutta* (Lokteff et al. 2013). Even when beavers are introduced outside of their native range, their ponds may improve habitat suitability for a variety of fishes. In South America, beaver ponds provide improved habitat for imperiled galaxiid fishes, and may provide a refuge against predation from introduced salmonids (Moorman et al. 2009).

Beaver ponds may also improve fish habitats by stabilizing channels and reducing bed and bank erosion as well as by retaining suspended sediment within active ponds (Compton et al. 2013, Puttock et al. 2018). By trapping these sediments, beaver ponds can also combat excessive nutrient loading due to agricultural waste, a major source of stream degradation (Fairchild and Velinsky 2006). Many stream-dwelling fishes are dependent on clean gravel substrates to spawn. Beaver ponds themselves therefore prove poor spawning grounds due to the large amounts of sediment they retain (Kemp et al. 2011).

Beavers can have negative impacts on fish communities and populations. In many cases, fishes in systems with active beaver ponds are less diverse than those inhabiting adjacent unimpounded reaches (Schlosser and Kalleymeyn 2000). This reduction in community diversity is often attributed to increased water temperatures and decreased oxygen levels, though these trends do not apply across all regions where beavers occur, or even for all ponds within a region (Schlosser and Kalleymeyn 2000, Kemp et al. 2011). Further, for many small-bodied fishes, beaver dams are a significant barrier to upstream movement (Compton et al. 2013). A 2011 meta-

analysis found that barriers to upstream fish passage were the most frequently-cited negative impact of beavers in the literature (Kemp et al. 2011).

Previous research has also shown beaver ponds to be suitable habitat for freshwater oligochaetes and other more sediment or low-DO tolerant macroinvertebrate taxa (Margolis et al. 2002, Fairchild and Velinsky 2006; Pliūraitė and Kesminas 2012). The freshwater oligochaete *Tubifex tubifex* is an intermediate host for the parasite *Myxobolus cerebralis*, the causative agent of whirling disease in salmonids (Gilbert and Granath 2001). *Myxobolus cerebralis* was first detected in North Carolina in 2015, and this has raised concerns about possible impacts to the state's trout fisheries (NCWRC 2015). However, there have been few studies of oligochaete distributions in southern Appalachian streams and it is unclear to what extent these streams afford habitat for tubificid worms capable of transmitting *Myxobolus* and other fish parasites. As beaver populations increase in North Carolina, it is possible that the increase in beaver impoundments may create hotspots for *Myxobolus* transmission.

These results highlight the role of biogeography in determining the response of fish populations to beaver dams. Although geographic and taxonomic context have been shown to be important to understanding the effects of beaver impoundments on streams, no studies have examined the response of diverse Southern Appalachian fish communities to beaver impoundments. Much of the research conducted on beaver effects on stream communities has been conducted in low-elevation, low-gradient streams, or in systems where beavers are not native (Jakes et al. 2007, Anderson and Rosemond 2010, Curran and Cannatelli 2014). These systems are typically warmer, more nutrient-rich, and have lower DO concentrations compared to Appalachian headwater streams. High elevation stream fish communities in this region are often comprised of species adapted to cool water temperatures and clean substrates. Because

Appalachian streams tend to be cooler, low-productivity systems, beaver-mediated changes to water temperature and DO may be more ecologically relevant in high elevation systems than compared to warmer low-elevation systems where low DO conditions are more common.

I predicted that headwater streams in Western North Carolina would see reduced species richness and diversity where active beaver ponds were present, compared to where ponds had been abandoned. I also predicted that certain fishes would be strongly associated with active beaver impoundments. Based on previous research, I also believed that active beaver ponds would provide ideal habitat for oligochaete worms. Finally, I predicted that active beaver impoundments would show lower DO saturation and higher water temperature when compared to surrounding reaches or inactive ponds. To test these predictions I collected fish community and water quality data from a number of blue ridge headwater streams during the summer of 2019.

Materials and Methods

Study Design

I sampled 16 headwater streams in the Catawba, New and Tennessee drainages in western North Carolina, displayed in figure 1. Sites were classified as active or inactive based on the apparent level of maintenance of the dam. Dams which appear to be maintained by resident beavers (i.e., have fresh branches incorporated, are free from major leaks) were classified as active. Dams that were breached and no longer impounded significant quantities of water were classified as inactive. For each dam, I selected four sites for habitat and fish sampling. Sites were 150-m reaches located 1) upstream of the impoundment in a free-flowing reach, 2) within the impoundment, 3) the tailrace, immediately downstream of the dam and 4) in a free-flowing reach

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located $\geq$300 m downstream of a beaver impoundment. If multiple impoundments or abandoned dams existed within a single site, the farthest downstream dam was used to calculate distances for tailrace and downstream samples. Downstream samples served as reference reaches to allow comparison between beaver-altered fish communities and unaltered fish communities. This followed the method of Smith and Mather (2013), who located control reaches > 100 m on the same stream from beaver impoundments to ensure the habitat was not influenced, but ensure geographical and physiochemical similarity between control and beaver reaches was maintained. I decided that upstream samples were not appropriate reference reaches, due to the difficulty many fishes have passing upstream of dams (Kemp et al. 2011)

Habitat Assessment and Sampling

In order to compute drainage area and compare forest cover among stream catchments, watershed boundaries were delineated at the downstream extent of sampling for each site using USGS Stream Stats (www.usgs.streamstats.gov). The amount of total forest cover (deciduous + coniferous + mixed) within the watershed for each site was then obtained using the 2016 National Land Cover Dataset in ArcMap 10.5.1 for Windows. A suite of water quality parameters was also collected from each sample reach. I measured water temperature, DO saturation, pH, NO_3^- concentration and specific conductance using a YSI Pro Series MultiParameter Meter (Yellow Springs Instruments, Yellow Springs OH).

Biotic Sampling

Fish and oligochaete samples as well as habitat and water quality data were collected during summer baseflow conditions at all sites. Study reaches were separated into mesohabitats (pool, riffle, run, or pond) and four different mesohabitats were sampled in each reach. Fish samples were collected from each of these mesohabitats. The four mesohabitats sampled in each sample reach were selected to incorporate as much habitat heterogeneity as possible.

Fishes were collected by backpack electrofishing using a Smith-Root LR-20B Backpack Electrofisher. Sampling effort in free-flowing reaches was standardized to ~100 s per mesohabitat (i.e., 400 s per reach). Four 100 s samples were also obtained from ponds and to account for habitat variability I attempted to sample from different mesohabitats within the pond including shorelines, woody debris and undercut banks. In both ponds and free-flowing reaches, a seine was also used to help isolate mesohabitats and reduce escapement. The deployment of the seine alongside backpack electrofishing allowed for the collection of a representative sample of the fish community that would not have been obtainable through backpack electrofishing alone (Meador et al. 1993).

All fishes were identified to species on site and returned to the water as quickly as possible following recovery. The only exception occurred at sites in the New River drainage, where multiple *Nocomis* spp. were present, but not readily identifiable to species in many cases. All *Nocomis* encountered at New River sites were therefore called *Nocomis* sp. in subsequent analysis. Any fish that did not recover from the electrofisher were euthanized with MS-222, preserved in non-denatured 95% alcohol, and vouchered in the Appalachian State University Zoological Collections. The total length of the first 30 individuals of each species from each study reach were measured and subsequent individuals were identified, enumerated and released.

Five benthic sediment samples were collected within each active or inactive pond using a bucket with the bottom removed and placed in undisturbed locations on the bottom of the pond. The substrate was then gently agitated by hand for 10 seconds and surface sediments, along with any vegetation or woody debris within the substrate were collected with a fine mesh aquarium net. Sediment samples were then transferred to clean glass or plastic jars and stored in a cooler until they could be transported to Appalachian State University. Sediment samples were washed through a 300-μm sieve and oligochaetes removed with forceps and stored in 95% non-denatured alcohol. Oligochaetes were transported to the Aquatic Parasitology Lab at Auburn University for identification and *Myxobolus* infection testing using PCR assays. In addition, all salmonid fishes were examined for any external signs of whirling disease (darkened caudal fin pigments, deformed craniums) in the field.

Data Analyses

I computed species richness (α) and Shannon-Weiner diversity (H') for each 100-second mesohabitat sub-sample using the *vegan* package in R 3.6.2 for Windows. The distribution of Shannon-Weiner diversities was strongly non-normal (Shapiro test: $W = 0.82255$, p-value < 0.001), and fish samples were clustered by site. Therefore, the package *lme4* was used to construct an *a priori* set of generalized linear mixed effects models (GLMMs) to examine the effect of beaver activity, sample reach (upstream, pond, tailrace, and downstream), forest cover, and other habitat variables on diversity and species richness. Backpack shocker time was also included as a co-variate in several candidate models, in order to account for any potential effects of deviating from the 100-second time limit imposed on the samples. Site was used as a random effect in all models. An appropriate distribution for a GLMM was then selected by examining

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QQ-plots generated using the *MASS* package. A gamma distribution with a log link function was selected as the most appropriate for the data. Model parameter estimates were generated by the Laplace approximation. All continuous variables not represented by percentages were standardized using z-scores to reduce parameter estimate bias, with the exception of relative proportion of forest cover, which was arcsin transformed. Any models which failed to converge were removed from the candidate model set. The candidate models were then compared using the package *AICcmodavg* to calculate second order Akakie's Information Criterion (AICc) to account for small sample sizes. Models with a $\triangle$AICc of < 2.0 were considered competitive models.

The distribution of species richness was also strongly non-normal (Shapiro test W = 0.81136, p-value < 0.0001), and clustered by site. GLMMs were therefore generated to examine the effect of the same covariates used to examine diversity on species richness. Site was once again used as a random effect in all models. Since the response variable was a count, a Poisson distribution with a log link function was selected as the most appropriate for the data. Model parameter estimates were again generated by the Laplace approximation. All continuous variables not represented by percentages were standardized using z-scores to reduce parameter estimate bias, with the exception of relative proportion of forest cover, which was arcsin transformed. Any models which failed to converge were removed from the candidate model set. The candidate models were then compared using the package *AICcmodavg* to calculate second order Akakie's Information Criterion (AICc) to account for small sample sizes. Models with a $\triangle$AICc of <2.0 were considered competitive models.

Fish species were divided into spawning and feeding guilds, and the relative frequency of these guilds was compared across activity levels and sample reach location. Following Jenkins

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and Burkhead (1994), Rhode et al. (2009) and the methods outlined in Sutherland et al. (2002), fishes were divided into benthic crevice spawners (BC), gravel spawners (G), benthic excavators (BE), benthic nest builders (BNB), and benthic nest associates (BNA). An additional category for species that attach eggs to vegetation (V) was added to accommodate species not considered by Sutherland et al. (2002). Fishes were also divided into feeding guilds: insectivore (I), piscivore (P), detritivore (D), or omnivore (O). Feeding guild assignments were made using evidence from available literature on life history and diet (www.fishbase.org, Jenkins and Burkhead 1994, Rhode et al. 2009). Where insufficient research was available on the life history of a species to reliably assign it to a spawning or feeding guild, the species was classified as unknown.

I conducted indicator species analyses on all fish species detected during the study, as well as each spawning and feeding guild, using the package *Indicspecies* (Indval.g, nperm = 9999, De Cáceres et al. 2010). Each sample reach position (upstream, pond, tailrace, and downstream) was considered a habitat type for both active and inactive streams. Groups were considered in the indicator species analysis, meaning that if a species had a higher affinity for a combination of different habitat types than for a single habitat type, that combination was considered significant. For the analysis of individual species, species that did not occur at more than one site were not considered valid indicators and were not reported in the final results. Associations between fishes categorized in unknown trophic groups and habitat types were also not reported. Raw numbers were converted to relative abundance to account for the influence of sites with high overall abundances for all indicator analyses.

Non-metric multidimensional scaling (NMDS) was also conducted both the full list of fish species in each sample, and a list of the breeding guilds present in each sample. To avoid the

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presence of samples in which no fish were detected, all four 100- second samples in a sample reach were combined and treated as a single sample. All abundances were converted to relative abundance to reduce the influence of highly abundant sites on the ordination. Pairwise dissimilarities were calculated using the Bray-Curtis method. This analysis was conducted using the *vegan* package in R 3.6.2 for windows.

I then used the packages lme4 and AICcmodavg to construct generalized linear mixed effects models to examine the effect of beaver activity, sample reach position (upstream, pond, tailrace, and downstream), forest cover, and other habitat variables on DO saturation and water temperature. Because water quality data were non-normally distributed, these models were then compared using second order Akakie's Information Criterion (AICc) to correct for small sample sizes. All continuous variables not represented by percentages were standardized using z-scores to reduce parameter estimate bias.

The number of samples which had oligochaetes present were compared based on activity using McNemar's test to account for the non-independence of bucket bottoms taken from the same site. The number of worms detected in each bucket bottom was then compared based on activity with a Mann-Whitney test in order to account for the strongly non-normal distribution of the data.

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Results

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Fish Species Richness and Diversity

The top GLMM selected found that species richness was best explained by main effects terms for dam activity status, elevation, and specific conductance. Although the 95% CIs around β estimates for elevation did not include zero, all other confidence intervals did. Therefore, while

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the model predicted decreasing species richness with increasing elevation with high confidence, and boxplots of species richness indicate that richness is universally lower at active sites, the model parameter estimate for activity cannot be confidently separated from zero (Figure 2). This indicates that a decrease in species richness with increasing elevation is the strongest factor determining species While The other top four models and the intercept only model and generally contained many of the same main effect terms (Table 3), One other competitive model with a △AICc of 1.9 also included a main effect term for sampling effort (electrofishing time). However, the top-ranked model is parsimonious and is consistent with our a priori hypotheses. Similarly, the top model for fish diversity found that diversity was best explained by main effects terms for dam activity and position, along with a main effect term for water conductivity. The 95% CIs around β estimates for sites in streams with inactive dams, as well as pond and tailrace sites did not include zero but all other parameter confidence intervals did (Table 4). This indicates a confident prediction by the model that streams with active beaver ponds have lower fish community diversity than streams with inactive beaver ponds, and that diversity in ponds and pond tailraces is lower than in surrounding unimpounded reaches. While the other terms in the model helped to more completely explain the data, their effect size estimates could not confidently be separated from zero. Boxplots of Shannon diversity by sample reach show that diversity was lower for active sites than inactive sites, and that diversity was generally lowest in pond and tailrace reaches (figure 3). One other competitive model with a △AICc of 0.99 included main effect terms for dam activity level and drainage area, along with an interaction of the two and a main effect term for water conductivity. However, the top model was still considered best since the two competitive models were equally parsimonious (Table 4).

Indicator Species Analysis

A Dufrene-Legendre indicator species analysis with groups found that 19 of 41 species that were significant indicators for habitat type, 10 occurred at more than one site (Table 1), and their specific associations are displayed in a heatmap (Figure 4). Associations between 4 of 6 sampled spawning guilds and one or more habitat types were also detected by indicator species analysis (Table 2). Of all the feeding guilds, only insectivores had a significant association with habitat type. Insectivores were associated with all habitat types except active beaver ponds (Indicator value = 0.667, p-value = 0.0097).

Ordination analysis

The ordination analysis showed no obvious clustering by dam activity or sample reach position for either the full species list (Figure 6), or the list of breeding guilds (Figure 7). The only factor which showed obvious clustering of fish communities was the full species list grouped by major drainage basin (Figure 8). Further discussion of the ordination results is therefore not warranted.

Physicochemical Parameters

The top models for DO and water temperature as selected by AICc both showed that the data were best explained by main effects terms for activity and position, along with their interaction. For oxygen, one other competitive model with a ΔAICc of 1.94 included an additional main effect term for sample elevation but was considered less parsimonious than the top model due to the additional term. An interaction term for which the confidence interval did not include zero

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indicated that inactive beaver ponds had higher oxygen levels than active beaver ponds. Boxplots of DO by sample reach show that oxygen saturation in active ponds is lower and more variable (78.99±13.28% mean and standard deviation) than in inactive ponds (87.62±2.33%) (Figure 9). Additionally, two interaction terms with confidence intervals not including zero indicated that water temperatures were higher for inactive ponds (18.65±2.42 °C) than active ponds (17.21±2.97 °C) and inactive upstream samples (18.78±2.15 °C) compared to active upstream samples (16.07±2.57 °C). Boxplots of water temperature by sample reach can be found in figure 10. Model parameter estimates and a comparison of the four top models with the null model can be found in tables 5 and 6.

Oligochaetes

The proportion of sediment samples in which oligochaetes were detected was significantly higher in active beaver ponds (McNemar's Test, $X^2 = 6.57$, p= 0.010) and worm densities were higher (Mann-Whitney test, W = 1015.5, p = 0.004). Mean oligochaete density in active ponds was 8.93 $\pm$ 24.8 worms$^{2-1}$ (mean ± SD). Oligochaetes were less abundant and variable in inactive ponds. Mean overall oligochaete density in inactive ponds was 1.96 ± 5.9 worms m$^{2-1}$. Although these results suggest that active beaver ponds provide habitat for oligochaetes and these habitats may act as transmission hotspots for *Myxobolus cerebralis*, I detected no abnormal salmonids during the study. The taxonomy and infection status of worms collected in the study has not yet been determined.

Discussion

Fish Community Structure

Results of diversity metrics and indicator species analyses suggested that beaver activity status as well as baseline biogeographic parameters including elevation and drainage area influence fish community composition. These effects were observed among streams supporting a diverse (N = 40 species) headwater fish community and represent among the first studies of beaver mediated impacts in southeastern upland streams.

Although the top model for fish species richness also included terms for dam activity, and water conductivity, only the elevation term had a 95% CI that did not contain 0. The β estimate for elevation predictably suggested that richness decreased with increasing elevation and this reflects the fact that higher elevation drainages naturally have smaller drainage areas. Watersheds with smaller areas generally support fewer fish species and this has been widely documented in southeastern streams (Watters 1992, Snodgrass and Meffe 1998). Additionally, higher elevation sites may have a larger number of downstream geographic barriers to fish movement and Schlosser and Kallemeyn (2000) considered this to be important to fish community structures in Great Lakes streams inhabited by beavers.

Though the confidence interval for the activity term in the species richness model included zero, median species richness in systems with active beaver ponds was universally lower than those with inactive ponds for all sample reaches. Reduced species richness observed in streams with active beaver ponds can be further illuminated by examining the results of ISAs. ISAs revealed that although some fishes were more likely to be detected in active and inactive beaver ponds, the majority of species sampled are more likely to be detected in free-flowing

stream habitats. Most of my top models indicated that streams with inactive beaver dams had higher diversity relative to streams with active beaver dams. In addition, pond and tailrace sites had reduced fish diversity compared to other sites although site effects were relatively small. Although Schlosser and Kallemeyn (2000) also found lower species richness in intact beaver impoundments compared with free flowing stream habitats, my findings are contrary to other studies (Snodgrass and Meffe 1998, Smith and Mather 2013).

Physicochemical Parameters

Reduced stream DO and elevated water temperatures are frequently associated with active beaver impoundments (Kemp et al. 2011). Although a priori hypotheses predicted that active beaver ponds might reduced headwater DO levels, the top model that included temperature predicted a slight temperature increase in inactive ponds compared to active ponds. Bouwes et al. (2016) similarly found that increased water depth in beaver ponds creates a thermal refuge characterized by cooler and more consistent temperatures. Although I did not collect time series data, temperature effects may warrant further study, since it appears dam-mediated thermal stabilization documented by Bouwes et al. (2016) from Oregon may also occur in North Carolina.

In many active beaver ponds, reduced DO is ascribed to increased temperature due to high residence times and high input of solar radiation at the surface of the impoundment (Kemp et al 2011). However, the prediction of elevated temperatures in inactive ponds conflicts with this explanation for reduced DO. Instead, it is perhaps more likely that the reduced DO in active ponds is attributable to high rates of decomposition and therefore biological oxygen demand,

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which has been proposed as a mechanism for hypoxia in other studies (Schlosser and Kallymen 2000). This may also explain the broad variation in DO in active ponds (mean and standard deviation = 79.0 ± 13.3) as ponds with differing amounts of leaf litter accumulation would experience highly variable rates of respiration due to microbial decomposition.

Indicator Analysis

Of the 10 fishes that were considered valid indicator species, only *Semotilus atromaculatus* and *Salmo trutta*, were significantly associated with active beaver impoundments. All other species in the analysis were associated with inactive impoundments or unimpounded reaches. Both species associated with active impoundments are known to frequently inhabit slow-moving, pool or pond-type habitats in many cases (Jenkins and Burkhead 1994). *Semotilus atromaculatus* is frequently found in pools, backwaters, and slow runs in southeastern streams but is considered to be intolerant of fine sediment because it needs clean gravel substrates for spawning (Jenkins and Burkhead 1994). *Semotilus atromaculatus* was also associated with habitats upstream of active beaver impoundments. *Semotilus atromaculatus* found upstream of active beaver impoundments were larger than those found in active ponds (Mann-Whitney test, $W = 751.00$, $p = 0.004$). Size differences observed between *S. atromaculatus* captured in pond and upstream reaches may indicate that spawning occurs in unimpounded habitats, and juveniles subsequently move into impoundments, since individuals captured in ponds were most frequently of size which indicated they were young of the year, while the majority of fish in unimpounded reaches were adults. At one site, 120 of 122 *Semotilus atromaculatus* captured in the pond < 40 mm TL, whereas only 1 individual < 60 mm was detected at all sampled upstream sites. Interestingly, Gilliam and Fraser (1987) conducted an experiment in which juvenile creek chubs avoided predation by adults of

their own species by hiding in a refuge area inaccessible to adults. The juveniles were more likely to leave the refuge to forage in the presence of predators if the density of *Tubifex* spp. worms available for consumption was higher. It seems likely therefore, that both the absence of large piscivorous adult creek chubs, and the presence of high densities of oligochaetes may make active beaver impoundments appealing habitat for juvenile creek chubs.

Salmo trutta inhabits a broad range of habitat types including both natural and artificial ponds (Jenkins and Burkhead 1994). Interestingly, Hägglund and Sjöberg (1999) reported that *Salmo trutta* were more abundant in unimpounded reaches relative to beaver ponds throughout the summer months in Scandinavian streams. This discrepancy may be attributable to the fact that *S. trutta* is native to Sweden (Bouwes et al. 2016). In my study, *S. trutta* was also significantly associated with sites upstream, downstream, and in the tailrace of beaver ponds. These associations are likely indicative of the ability of *S. trutta*, like other salmonids, to pass over intact beaver dams (Lokteff et al. 2013). In addition to associations with habitats adjacent to active impoundments, *S. trutta* was associated with sites downstream of inactive beaver impoundments. The majority of downstream sites represent habitats that are largely unaltered by beaver activity, and thus this association may not be an effect of stream impoundment.

The only other species that had a significant association with streams where active beaver ponds were present was *Cottus bairdi*. However, *C. bairdi* was associated with all habitat types except active beaver impoundments across both activity levels. Active beaver ponds likely provide poor habitat for *Cottus bairdi*, a species that also unimpounded stream habitats with clean substrate for spawning and at all life history stages and is generally considered intolerant of sedimentation (Jenkins and Burkhead 1994). I therefore consider this broad range of associations

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to represent intolerance of beaver impoundments. Freshwater sculpins require unimpounded stream habitats with clean substrate at all life history stages.

The remaining 7 indicator species were associated only with sites in streams with inactive beaver dams. *Oncorhynchus mykiss* was associated with all sites in streams with inactive dams. Although it is not native to the southern Appalachians, *Oncorynchus mykiss* typically inhabits cooler, high-gradient streams and swift current has been shown to be more important to the species than to *S. trutta* (Lewis 1969). A suite of 4 other fishes was also associated with all positions at inactive streams: *Campostoma anomalum, Chrosomus oreas, Luxilis coccogenis,* and *Nocomis sp*. Three species, *Campostoma anomalum, Chrosomus oreas*, and *Luxilis coccogenis*, spawn over nests constructed by *Nocomis* chubs and two other species of chub, *Nocomis leptocephalus* and *Nocomis micropogon* were associated with inactive dam imoundment and tailrace site. Male *Nocomis* construct nests using small stones placed into a large (1+ m^2) mounds and females deposit eggs within these structures (Jenkins and Burkhead 1994). Furthermore, *N. micropogon* and *N. leptocephalus* are thought to prefer high-gradient streams with coarse substrates, and *N, leptocephalus* is infrequently found over silt substrate (Jenkins and Burkhead 1994). Though *Nocomis* and *Semotilus* are known to be able to cope with a degree of sedimentation, stream reaches impounded by beavers are thus unlikely to provide any of the coarse substrates needed by *Nocomis* due to their complete burial below fine sediment (Sutherland et al. 2002). Many *Nocomis* nest associates, including *Chrosomus oreas* are obligate participants in the nesting symbiosis and will not lay eggs in the absence of chub nests (Jenkins and Burkhead 1994, Peoples and Frimpong 2016). This association likely explains the results of breeding guild-focused indicator analyses.

Benthic nest associates were significantly associated with all sites in streams with inactive beaver dams. This indicates that fishes with life histories linked to the presence of *Nocomis* or *Semotilus* nests indirectly require coarse, sediment-free substrates characteristic of free-flowin streams in this region. Benthic nest builders were associated with all sites in streams with inactive dams, as well as with active ponds and sites upstream of active ponds. The association with sites in streams with active beaver dams may be driven by the presence of *Semotilus* at these sites, whereas *Nocomis* presence likely indirectly drove associations with inactive habitats. Benthic crevice spawners were associated with all sites and habitat types except active ponds. These species included fishes like *Etheostoma flabellare* and *C. bairdi*, that build nests under flat rocks, as well as *Cyprinella galactura,* a species that spawns in cracks in bedrock or boulders. All of these species require clean substrate with open interstices to complete their life cycle, and thus their absence from active ponds is unsurprising. Species that attach their eggs to vegetation included 2 species, *Etheostoma blenniodies* and *Etheostoma swananoa*, that attach their eggs to emergent vegetation or aquatic macrophytes (Jenkins and Burkhead 1994). Their increased prevalence in streams with inactive dams likely reflects a preference of the adults of both darter species for sediment-free substrate, and is likely not related to spawning habitat availability.

The preference for clean substrate may also be the driving mechanism behind the association between insectivores and habitat other than active impoundments. Many of the insectivore fishes in the analysis are species like *C. bairdi*, which feed on small invertebrates like chironomids in the interstices (Jenkins and Burkhead 1994). Active impoundments probably impede this behavior, and thus deter these species from inhabiting beaver ponds.

Oligochaetes

Genetic testing to confirm the identity of oligochaetes and the presence or absence of *Myxobolus* and other fish parasites is ongoing. However, the absence of any abnormal salmonids from the surveyed streams is an encouraging sign that active beaver ponds are unlikely to be currently facilitating the transmission of myxozoan parasites in North Carolina streams. Although no transmission appears to be currently affecting trout populations associated with beaver ponds, it is clear that active ponds provide higher quality oligochaete habitat than inactive ponds. The presence of freshwater oligochaetes in beaver ponds is consistent with the results of previous studies of pond invertebrate communities (Margolis et al. 2002). The results of the ongoing genetic testing will prove vital in further assessing the potential of beaver ponds to facilitate the spread of fish parasites.

Management Implications

These data represent the first study to examine beaver effects on stream fish communities in the Southern Appalachian Mountains. Although intact beaver ponds in this study supported less diverse fish communities, this does not mean that they are inherently poor habitat. Preferences of some species for streams with active beaver impoundments may reflect the fact that many of the region's fishes likely co-evolved with beavers, and that beaver impoundments may be integral to the life history of these species. When managers are deciding whether or not to allow beavers to colonize a reach of stream, it is crucial that the life history and trophic ecology of the fishes under management be considered. My data also show that a trait-based approach to assessing the impact of beavers on native or introduced fishes is likely an effective way to inform management decisions. Beavers are increasingly being used in stream restoration programs and

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regionallybased studies that consider how beavers implement changes to stream water chemistry and fish populations are need to better understand how to manage stream communities in the southern Appalachian Mountains.

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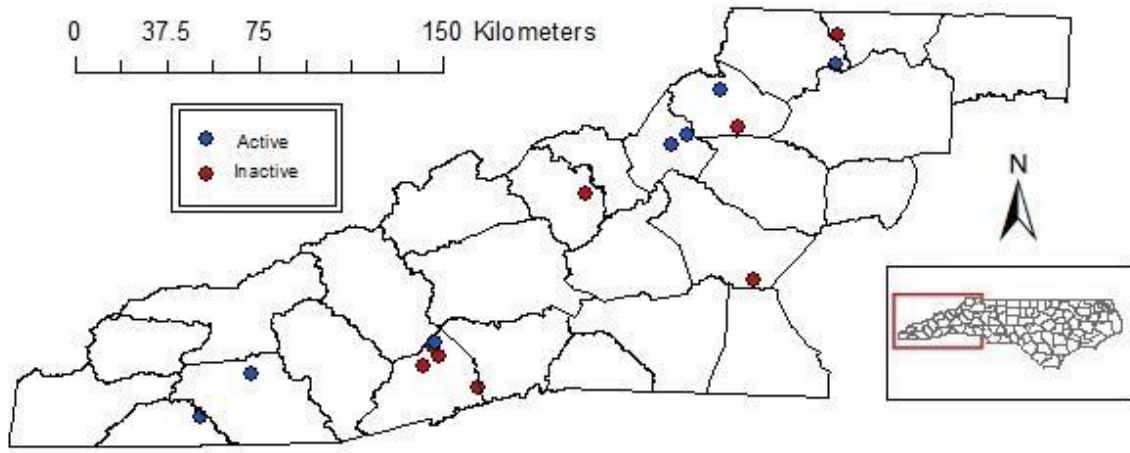
130-137

Figures and Tables

Figure 1. Location of survey sites. Blue points represent sites with active beaver dams, and red points represent sites with inactive dams. Inset map shows area of detail in western North Carolina.
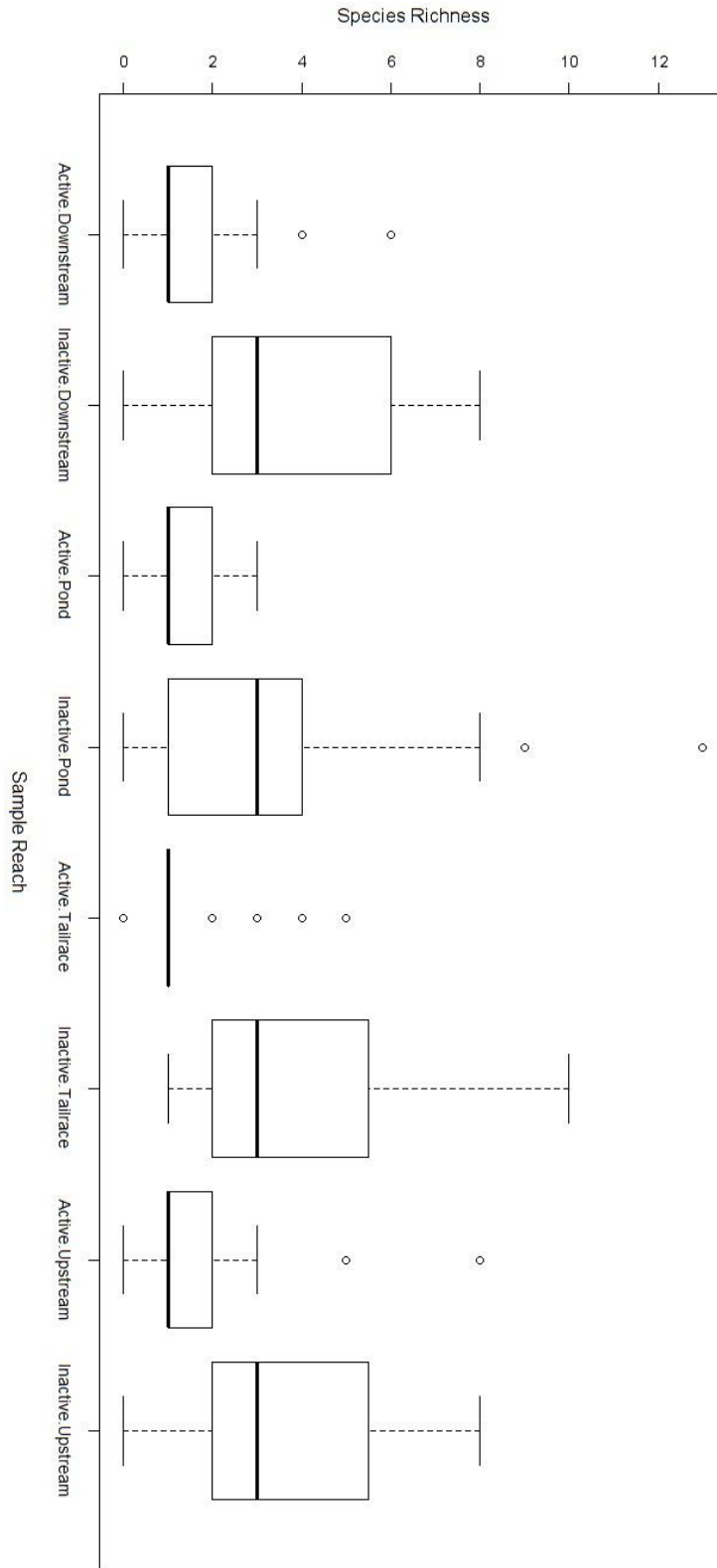
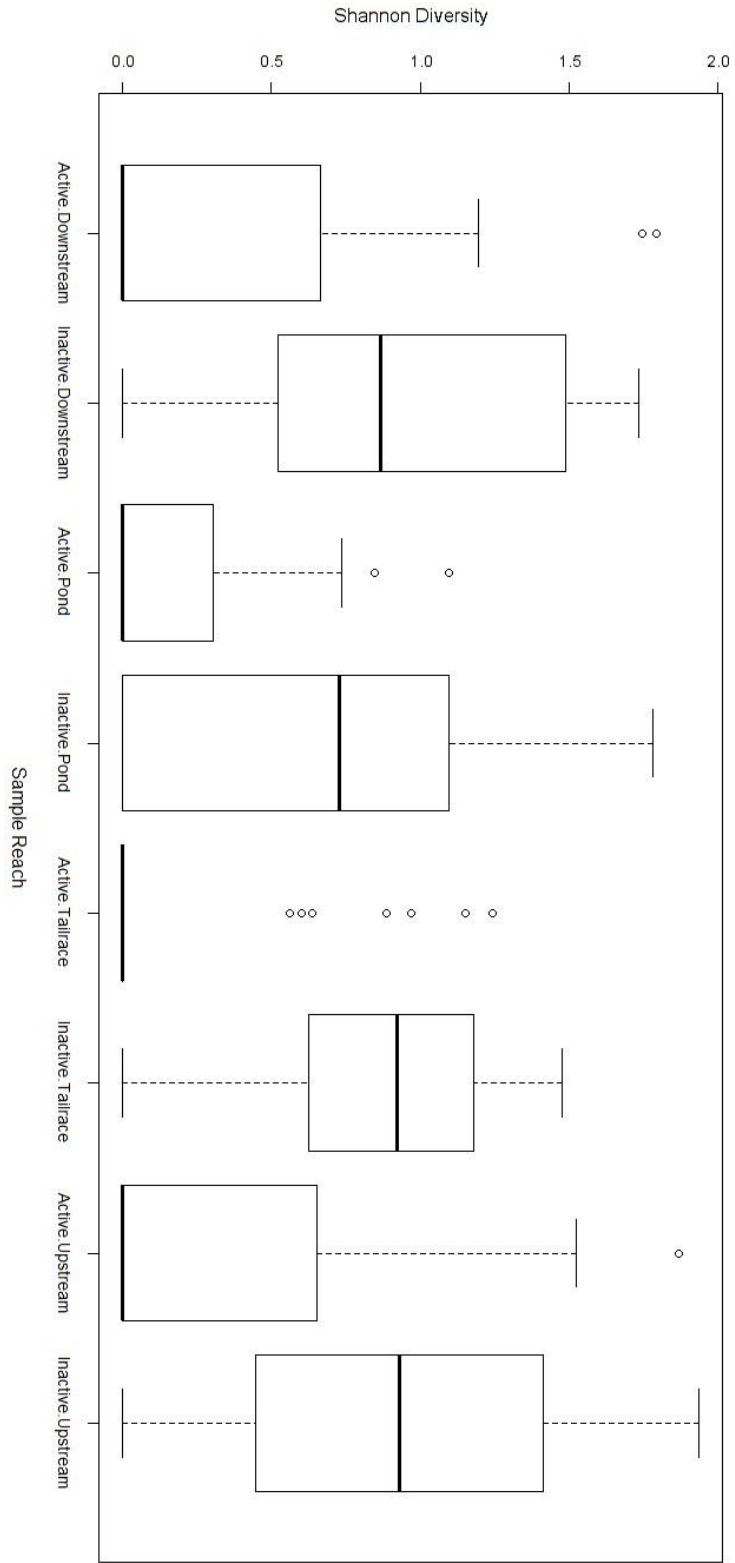Figure 2. Boxplots of species richness by sample reach

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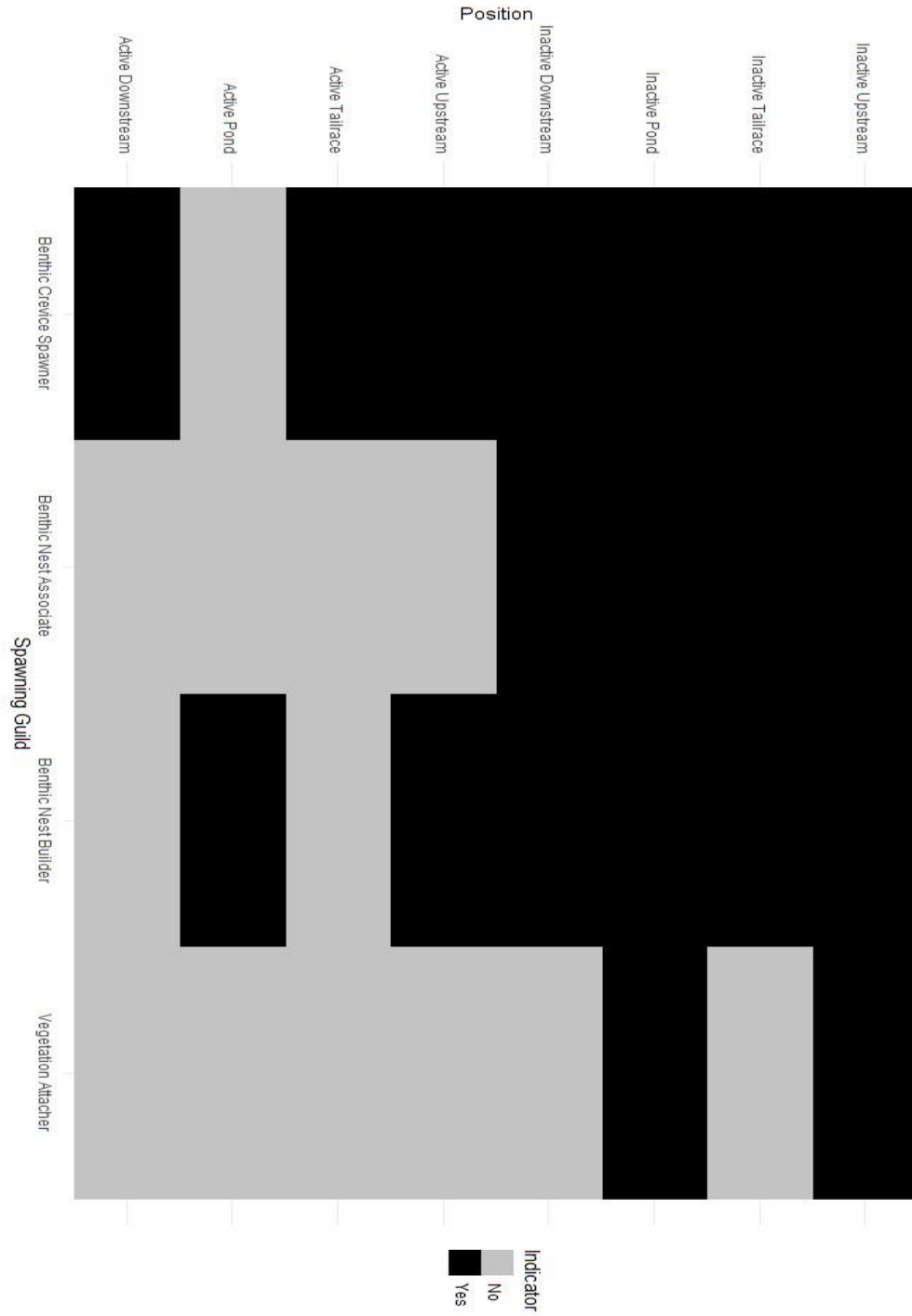Figure 3. Boxplots of Shannon diversity index by sample reach

Figure 4. A heatmap displaying the results of an indicator species analysis for breeding guilds. All guilds included had significant associations with their habitat (p < 0.05) and occurred at multiple sites.
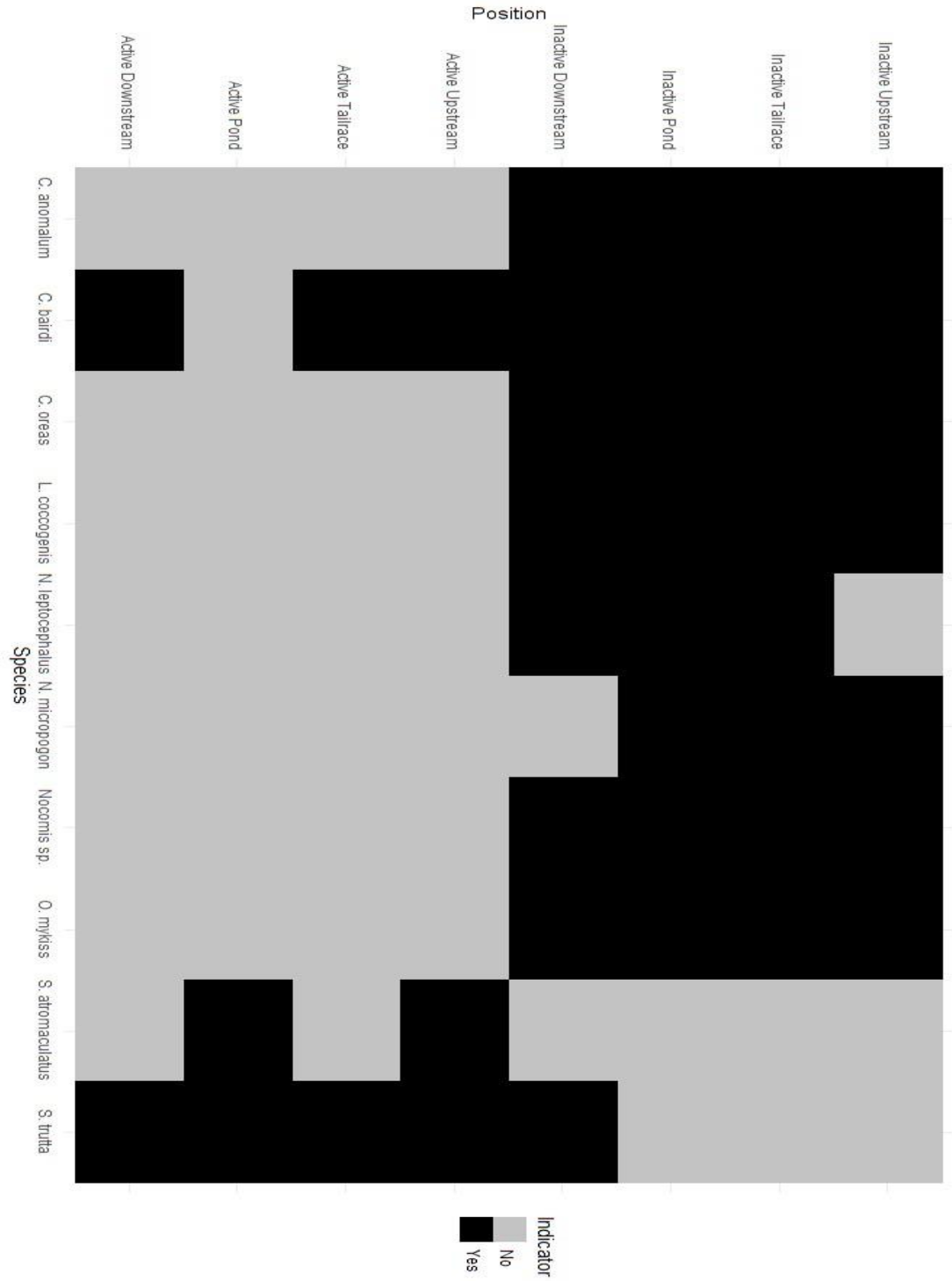
Figure 5. A heatmap displaying the results of an indicator species analysis for species. All species included had significant associations with their habitat (p < 0.05) and occurred at multiple sites.
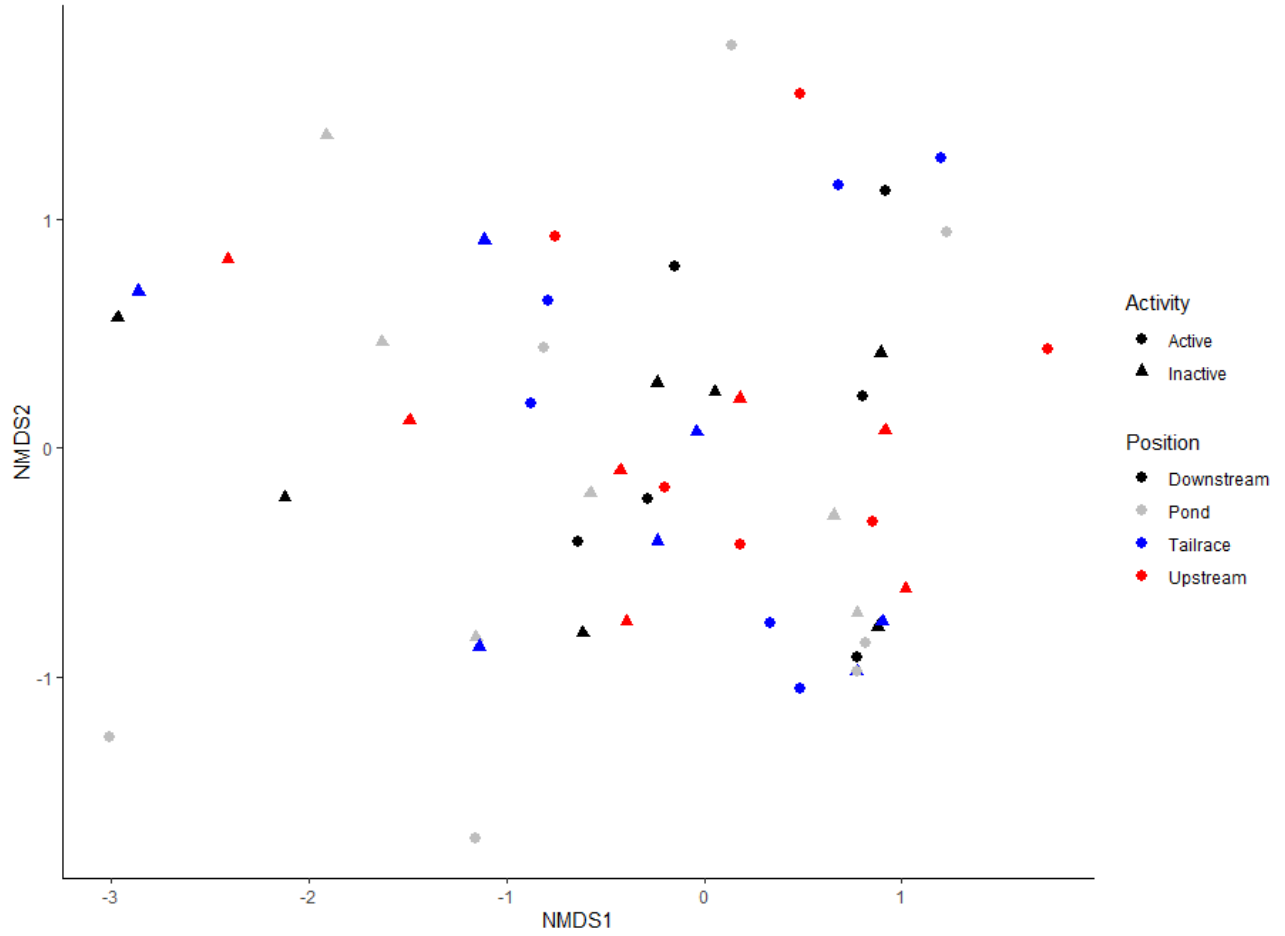
Figure 6. An NMDS plot for the full list of species in the study, with sites assigned to their activity level and position. Stress value = 0.12
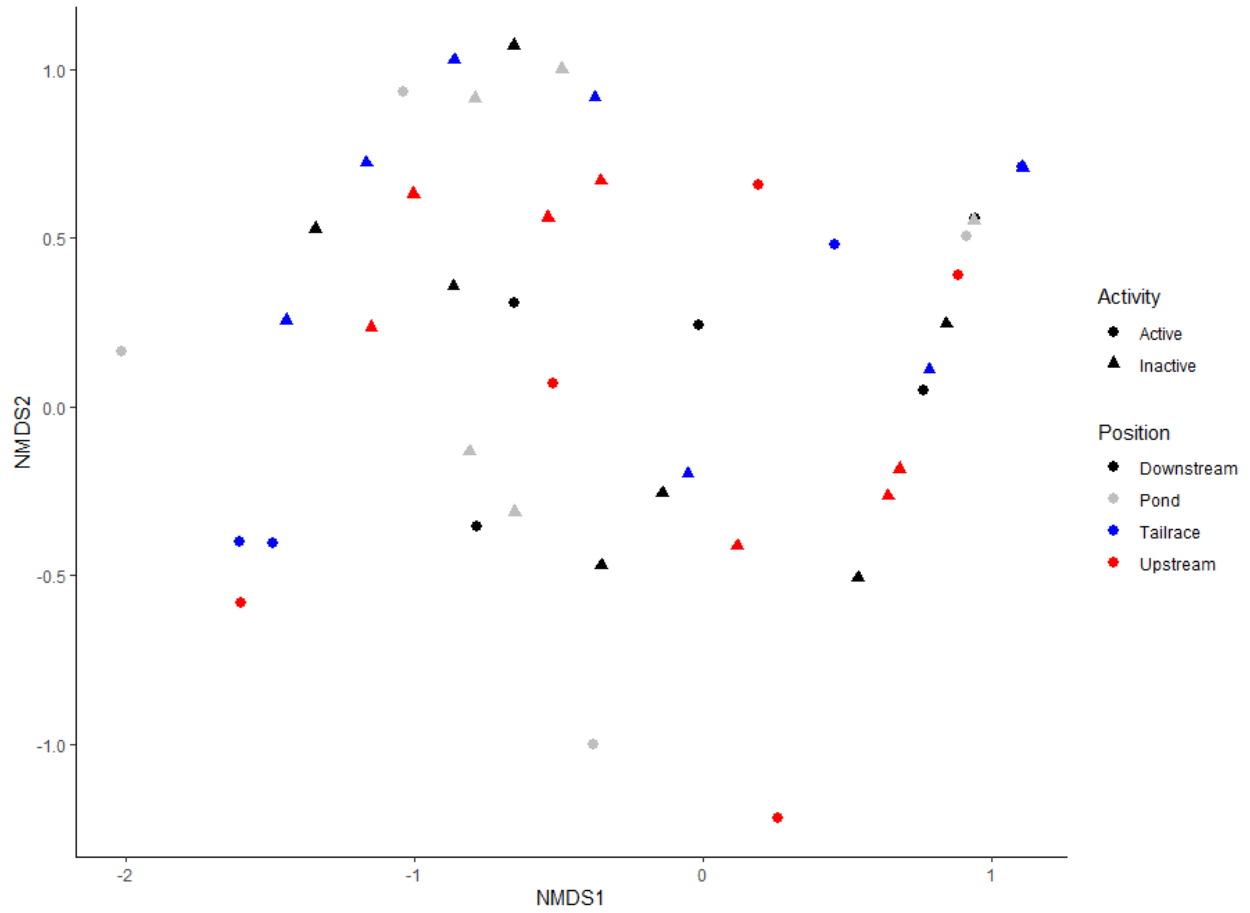
Figure 7. An NMDS plot based on assignment of each species to its breeding guild. Each sample is assigned to its activity level and sample reach position. Stress value = 0.11.
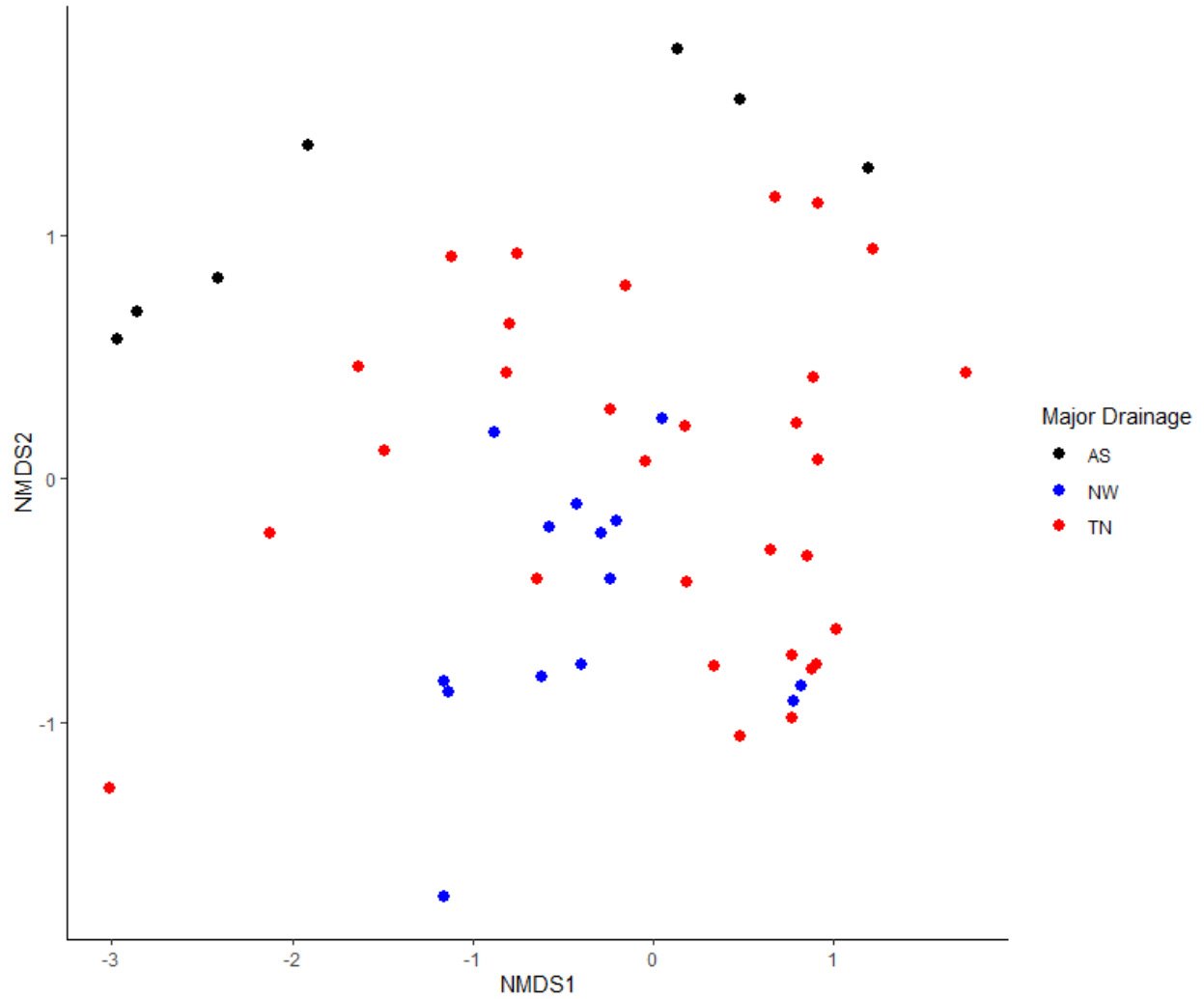
Figure 8. An NMDS plot based on all fish species in the analysis, with samples assigned to their major drainage: Atlantic Slope (AS), New (NW), or Tennessee (TN). Stress value = 0.12.
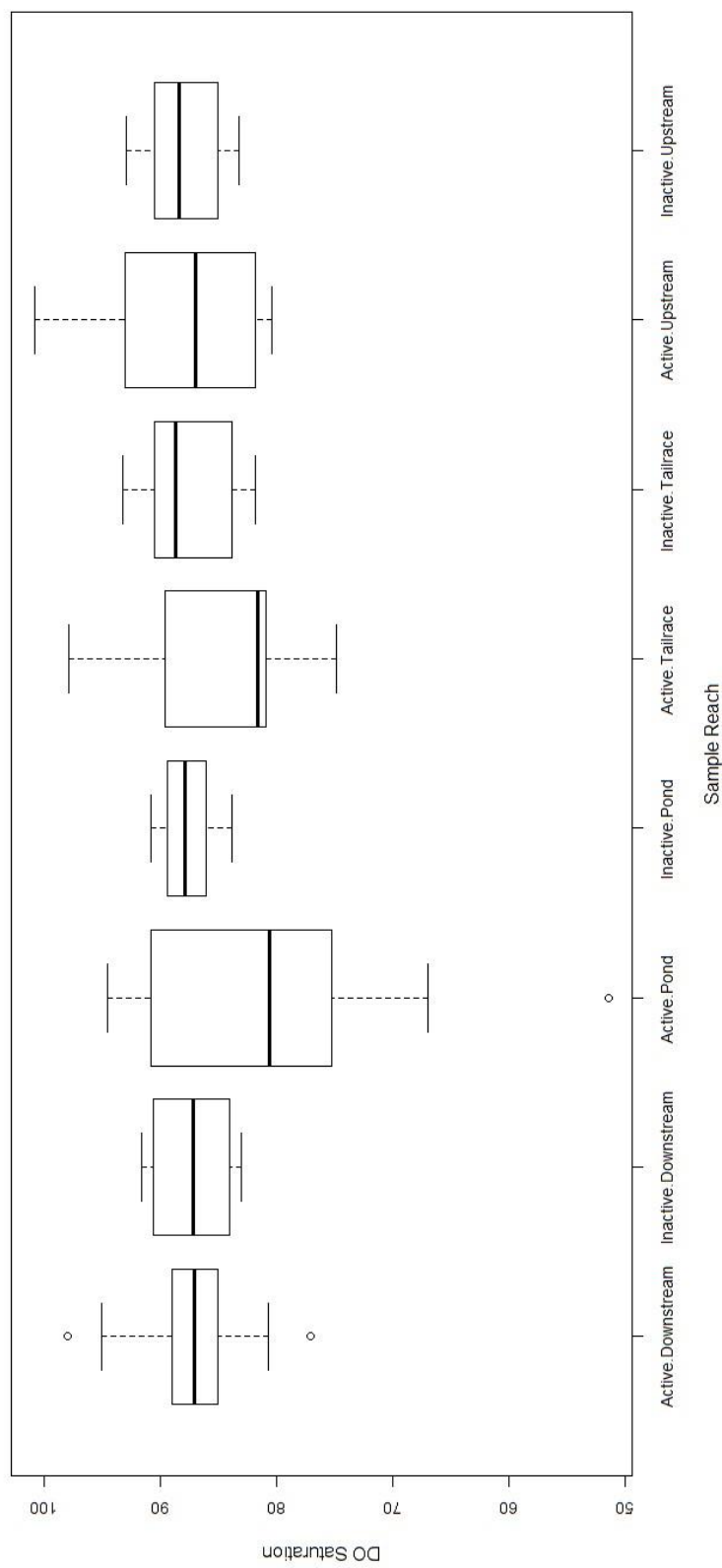
Figure 9. Boxplots of DO saturation by sample reach.

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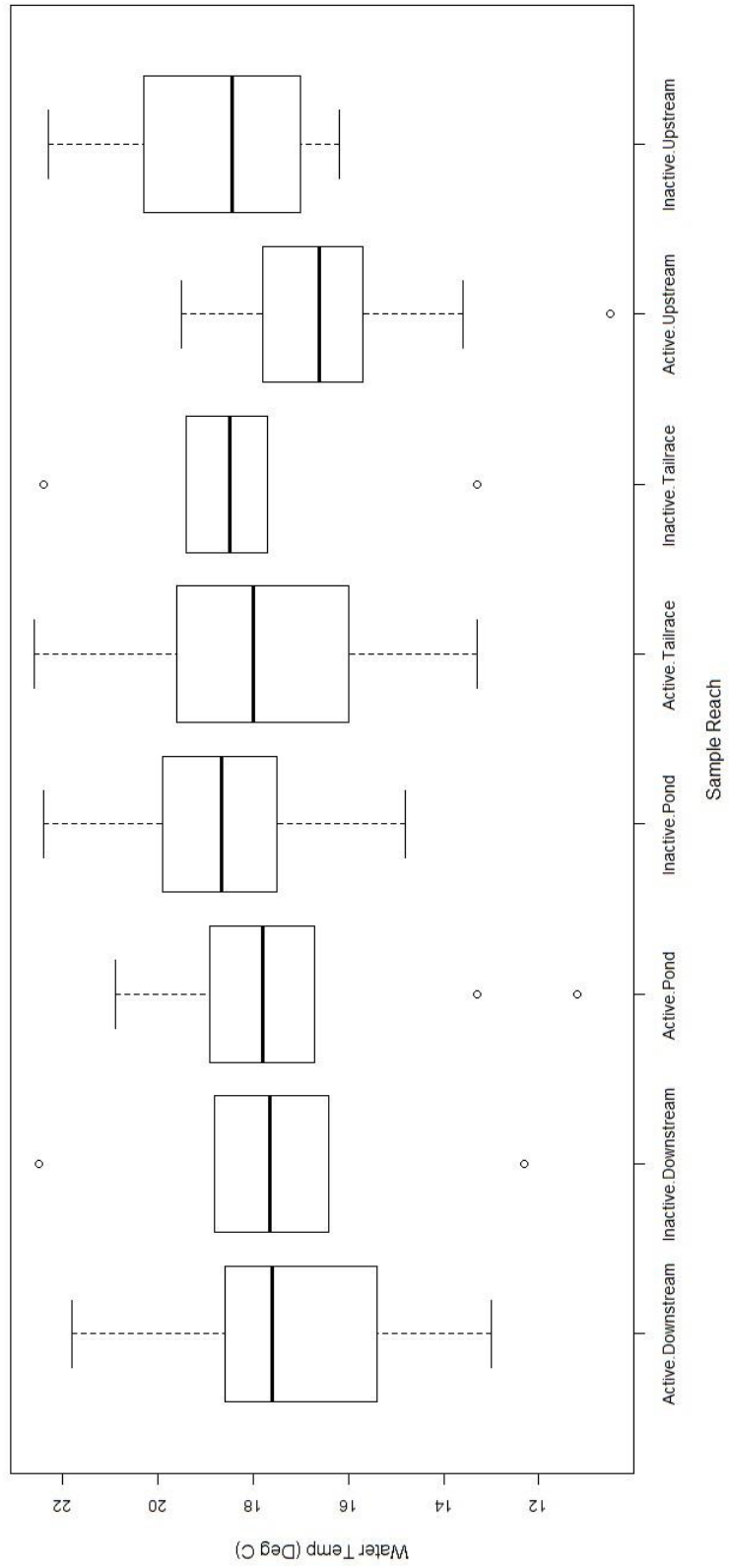
Figure 10. Boxplots of water temperature by sample reach.

Table 1. A list of indicator species detected by indicator species analysis. Indicator statistics and permutational p-values for each species are provided above. The specific habitat associations of each species can be found in Figure 1.

| Species	Indicator Statistic	p-value
Campostoma anomalum	0.497	0.0001
Chrosomus oreas	0.339	0.0051
Cottus bairdi	0.512	0.0040
Luxilis coccogenis	0.450	0.0001
Nocomis leptocephalus	0.357	0.0027
Nocomis micropogon	0.301	0.0268
Nocomis sp.	0.341	0.0038
Oncorhynchus mykiss	0.401	0.0018
Salmo trutta	0.494	0.0040
Semotilus atromaculatus	0.369	0.0046

Table 2. A list of spawning guilds with significant habitat associations detected by indicator species analysis. Indicator statistics and permutational p-values for each guild are provided above. The specific habitat associations of each guild can be found in Figure 1.

Spawning Guild	Indicator Statistic	p-value
Vegetation Associate	0.275	0.0238
Benthic Nest Builder	0.477	0.0001
Benthic Nest Associate	0.664	0.0011
Benthic Crevice Spawner	0.551	0.0036

Table 3. Parameter estimates for the top model describing fish species richness in streams with active and inactive beaver dams in western North Carolina mountain streams. Site was used as a random effect in all models. Bold text indicates terms with 95% CIs around the parameter estimate which did not include zero.

Model	Parameters	β estimate	95% CI
Species richness	Activity(Inactive)	0.521	-0.161, 1.007
	Elevation	**-0.432**	**-0.087, -2.453**
	Activity(Inactive):Elevation	0.186	-0.382, 0.754
	Conductivity	0.233	-0.007, 0.473

Model	Ka	ΔAICc[b]	AICcWt[c]
Species richness ~ Activity * Elevation + Conductivity	6	0	0.41
Species richness ~ Activity * Area + Conductivity	6	0.98	0.25
Species richness ~ Activity * Elevation+ Shocker Time+ Conductivity	7	2.08	0.15
Species richness ~ Activity * Position + Landuse + Conductivity	6	2.89	0.10
Null model: Species richness	2	74.44	0.00

Table 4. Model parameter estimates for fish Shannon-Weiner diversity in streams with active and inactive beaver dams in western North Carolina mountain streams. Site was used as a random effect in all models. Bold text indicates terms with 95% CIs around the parameter estimate which did not include zero.

	Parameters	β estimate	95% CI
Shannon Diveristy + 1	**Activity(Inactive)**	**0.335**	**0.012, 0.657**
	Position(Pond)	**-0.083**	**-0.154, -0.011**
	Position(Tailrace)	**-0.082**	**-0.154, -0.011**
	Position(Upstream)	-0.028	-0.100, 0.044
	Conductivity	0.057	-0.086, 0.200

Model	Ka	ΔAICc[b]	AICcWt[c]
Shannon Diversity + 1 ~ Activity + Position + Conductivity	8	0	0.50
Shannon Diversity + 1 ~ Activity + Position + Conductivity + Shocker Time	8	1.9	0.18
Shannon Diversity + 1 ~ Activity * Area + Conductivity	7	7.0	0.10
Shannon Diversity + 1 ~ Activity * Landuse + Conductivity	5	7.3	0.07
Null model: Shannon Diversity + 1	3	20.1	0.00

Table 5. Model AICc and parameter estimates for the top model describing DO saturation in western North Carolina streams with active and inactive beaver dams. Site was used as a random effect in all models. Bold text indicates terms with 95% CIs around the parameter estimate which did not include zero.

	Parameters	β estimate	95% CI
DO Saturation	Activity(Inactive)	-0.002	-0.116, 0.111
	Position(Pond)	**-0.108**	**-0.132, -0.084**
	Position(Tailrace)	-0.013	-0.038, 0.011
	Position(Upstream)	0.012	-0.012, 0.036
	Activity(Inactive):Position(Pond)	**0.113**	**0.075, 0.151**
	Activity(Inactive):Position(Tailrace)	0.019	-0.019, 0.058
	Activity(Inactive):Position(Upstream)	-0.003	- 0.040, 0.035

Model	Ka	ΔAICc[b]	AICcWt[c]
DO Saturation ~ Activity * Position	10	0	0.48
DO Saturation ~ Activity * Position + Elevation	11	1.94	0.18
DO Saturation ~ Activity * Position + Area	11	2.03	0.17
DO Saturation ~ Activity * Position + Landuse	11	2.11	0.16
Null model: DO Saturation	3	80.7	0.00

Table 6. Model AICc and parameter estimates for the top model describing water temperature in western North Carolina streams with active and inactive beaver dams. Site was used as a random effect in all models. Bold text indicates terms with 95% CIs around the parameter estimate which did not include zero.

Dependant Variable	Parameters	β estimate	95% CI
Temperature	Activity(Inactive)	0.008	-0.217, 0.232
	Position(Pond)	-0.012	-0.034, 0.010
	Position(Tailrace)	**0.034**	**0.012, 0.056**
	Position(Upstream)	**0.011**	**-0.100, -0.057**
	Activity(Inactive):Position(Pond)	**0.080**	**0.045, 0.115**
	Activity(Inactive):Position(Tailrace)	0.018	-0.023, 0.046
	Activity(Inactive):Position(Upstream)	**0.157**	**0.123, 0.192**

Model	Ka	ΔAICc[b]	AICcWt[c]
Temp ~ Activity * Position	10	0	0.44
Temp ~ Activity * Position + Area	11	0.63	0.32
Temp ~ Activity * Position + Elevation	11	1.20	0.24
Temp ~ Position	11	75.35	0.00
Null model: Temp	3	97.60	0.00

Vita

Samuel Frederick Fritz was born in Cameron, North Carolina to Gayge Eberbach and Frederick Royal Fritz. He began his college education at Appalachian State University in the fall of 2013, graduating in December 2017 with a Bachelor of Science degree in Biology. In fall of 2018, he enrolled in the graduate school at Appalachian State University to peruse a Master of Science degree under Dr. Michael Gangloff, with a concentration in ecology and evolutionary biology.

Sam is a member of both the North Carolina chapter and national membership of the American Fisheries Society, as well as Sigma Xi and the Ecological Society of America. In his free time, he can be found hiking, camping, gardening, or fishing, all in the company of his dog, Pisgah.