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South Atlantic Stream Fish Assemblages: Multi-Scale Structuring Factors, Trait Associations and Channelization, and Responses to Dam Removal

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SOUTH ATLANTIC STREAM FISH ASSEMBLAGES:
MULTI-SCALE STRUCTURING FACTORS,
TRAIT ASSOCIATIONS AND CHANNELIZATION,
AND RESPONSES TO DAM REMOVAL

A Dissertation
Presented to
the Graduate School of
Clemson University

In Partial Fulfillment
of the Requirements for the Degree
Doctor of Philosophy
Wildlife and Fisheries Biology

by
Cathy Aubrey Marion
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ABSTRACT

South Atlantic coastal plain streams are unique and understudied freshwater environments that provide crucial habitats for a wide range of aquatic taxa. In Chapter 1, we investigated patterns in fish assemblages across South Carolina's coastal plain, and developed statistical models to identify the dominant multi-scale abiotic environmental factors that influence assemblage structure. Our analyses indicated the presence of four predominant fish assemblages that commonly occur in the South Atlantic coastal plain, which we termed the: 1) fluvial, 2) eastern mudminnow, 3) centrarchid, and 4) non-fluvial assemblages. Natural geographic gradients and instream habitat parameters associated with velocity, channel form, stream size, and depth played a greater role in distinguishing fish assemblages than catchment land cover, and these instream habitat parameters showed weak relationships with anthropogenic land cover conditions. We proposed four possible explanations as to why geographic gradients and instream parameters have greater explanatory power than catchment land cover parameters in determining coastal plain fish assemblage structure, and why instream factors may not be strongly linked to land cover factors. Explanations included: 1) a sustained dynamic equilibrium among catchment, riparian, and instream conditions over time may encourage assemblage partitioning among differential instream habitats, 2) past-landscape disturbances may have greater influence on current instream habitats and fish assemblage structure, 3) weak relationships between catchment land cover and instream habitats may be common in low elevation regions, and 4) seasonal hydrologic patterns may dominantly influence instream habitat conditions and fish assemblage structure. This

study adds essential information towards a better understanding of how South Atlantic coastal plain fish assemblages respond to abiotic factors across multiple spatial scales. Such knowledge will help improve management and conservation strategies, as well as assist in the development of appropriate indicators for standardized evaluations of ecological integrity.

We investigated the impacts of channelization on South Atlantic coastal plain stream habitats and fish assemblages in Chapter 2. Hundreds of miles of coastal plain streams have been dramatically altered by channelization over the last 200 years for agricultural, silvicultural, or other anthropogenic endeavors. Although there is some evidence to the contrary, the impacts of channelization on stream habitats and fish assemblages of different regions have generally been negative. Previous research on the impacts of channelization on fishes has largely focused on changes in traditional measures of taxonomic diversity and assemblage-based analyses. However, trait-based analyses offer an alternative approach for assessing fish assemblage response to channelization that may enhance our understanding of disturbance/response patterns in South Atlantic coastal plain streams. We categorized sampled streams a priori into 4 channel types based on observations of their gross channel morphology: 1) single channel non-channelized streams, 2) maintained channelized streams, 3) unmaintained (> 5years) channelized streams, and 4) braided swamp-like non-channelized streams. We performed a series of statistical tests to identify significant instream habitat differences among channel types, and evaluated differences in fish assemblages using both taxonomic and trait-based analyses. Our results indicated that channelization significantly influences the

instream physicochemical habitat conditions of South Atlantic coastal plain streams, and in turn influences patterns of fish assemblage structure. Maintained channelized streams retained higher average velocities than unmaintained channelized streams, but both types of channelized streams had fewer structural habitat components, greater indications of water quality degradation, and lacked floodplain connectivity in comparison to unchannelized streams. We found no difference in fish taxonomic diversity metrics among channel types, and taxonomic assemblage-based analyses revealed limited information regarding structural associations. In contrast, our trait-based analysis elucidated species differences among all channelized and non-channelized channel types; principal differences were found in habitat preference, and body size/reproductive ecology. Single channel non-channelized streams were typified by a suite of native rheophilic species, while braided swamp-like streams hosted native rheophobic fishes with high tolerance to low-flow habitats. Although actively maintained channelized streams retained fluvial habitats, they failed to support native rheophilic species. Instead, they were typified by fishes with opportunistic/colonizing life histories common to aquatic systems with low environmental stability and high abiotic stress. Unmaintained channelized streams were typified by predatory species, reflecting the potential for these streams to undergo seasonal dewatering events. Unmaintained channelized assemblages were otherwise similar to those of braided-swamp like streams, indicating the potential for biotic recovery of channelized streams over time. Our study suggests that trait-based analyses may be particularly well suited to elucidating information on ecological response to environmental disturbances in the South Atlantic coastal plain, and their use

in conjunction with taxonomic analyses should provide a fruitful avenue for developing and testing ecological theory of fish assemblage organization in this region.

Dam removal is considered an effective tool for restoring ecological integrity to rivers and streams, yet few studies have investigated the impacts and recovery of fish assemblages after dam removal(s), and virtually no published research has emerged from dam removals in the southeastern U.S. The study presented in Chapter 3 examined the effects of two dam removals on instream habitat, fish metrics, and fish assemblage structure of Twelvemile Creek, a tributary to the Lake Harwell Reservoir, located in Pickens County, South Carolina. Our results indicated that the bulk of instream habitat changes occurred within 1-year of each dam removal; major geomorphic adjustments led to dramatically increased flow rates and shifts from fine to coarse/bedrock substrates in both former impoundments. However, we found no significant instream habitat changes in downstream free-flowing sites despite field observations that indicated persisting deposited sediment for the duration of the study, with greater deposition in the vicinity of the downstream-most removed dam. Previously lentic-dominated fish assemblages at former impounded sites generally shifted to a lotic-dominated structure within 6-months (upper-removed dam), and 1-1.5 years (lower-removed dam) after dam removal. Despite these prominent assemblage shifts, we found impacts on benthic invertivore density at sites flanking the upper-removed dam at 2.5-years post dam removal, and impacts on total density, richness, benthic invertivore density, and native centrarchid density at sites flanking the lower-removed dam at 2-years post dam removal. These findings suggested that multiple dam removals had a cumulative downstream increase in negative impacts on

fish assemblages. We also observed a sharp increase in non-native density following the removal of the lower-most dam, led by captures of *Micropterus henshalli*, a non-native species introduced to the downstream Lake Hartwell reservoir in the 1980s that is known to reduce native *Micropterus coosae* populations through introgressive hybridization. We routinely captured *Micropterus coosae* at all sample sites both before and after dam removals, whereas we only captured *Micropterus henshalli* in post dam removal samples. As such, our study elucidated the potential for tributary dams to act as barriers that protect native lotic species from the influence of downstream reservoir taxa; such phenomena may be exacerbated in southeastern U.S., where impoundment and reservoir density is extremely high. Although dam removal can have ecological trade-offs and short-term disturbance impacts, we demonstrated that dam removal can also reverse many of the negative impacts dams have on fish assemblages, primarily through the restoration of high-quality lotic habitats required by native riverine species. Our findings suggest that fish assemblages in high-gradient southeastern U.S. systems are likely to recover once habitat disturbances and sediment loads are fully reduced, assuming highly vulnerable or sensitive species are not at risk.

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CHAPTER ONE

MULTI-SCALE INFLUENCES ON THE TAXONOMIC STRUCTURE OF
SOUTH ATLANTIC COASTAL PLAIN FISH ASSEMBLAGES

Abstract

South Atlantic coastal plain streams are unique and understudied freshwater environments that provide crucial habitats for a wide range of aquatic taxa. We investigated patterns in fish assemblages across South Carolina's coastal plain, and developed statistical models to identify the dominant multi-scale abiotic environmental factors that influence assemblage structure. We performed hierarchical agglomerative clustering, indicator species analysis, and non-metric multidimensional scaling analyses on fish assemblage data collected at 208 wadeable coastal plain streams to identify and describe the predominant fish assemblages that commonly occur in the region. We used classification random forests to identify the multi-scale abiotic variables that best distinguish the habitats of faunal associations we identified. Our analyses indicated the presence of four predominant fish assemblages that commonly occur in the South Atlantic coastal plain, which we termed the: 1) fluvial, 2) eastern mudminnow, 3) centrarchid, and 4) non-fluvial assemblages. Assemblage names were assigned based on the prevailing taxonomic and/or ecological attributes of the species with the highest indicator values for each group. Natural geographic gradients and instream habitat parameters associated with velocity, channel form, stream size, and depth played a greater role in distinguishing fish assemblages than catchment land cover and stream network parameters, and these instream habitat parameters showed weak relationships

with anthropogenic land cover conditions. We proposed four possible explanations as to why geographic gradients and instream parameters have greater explanatory power than catchment land cover parameters in determining coastal plain fish assemblage structure, and why instream factors may not be strongly linked to land cover factors. Explanations included: 1) a sustained dynamic equilibrium among catchment, riparian, and instream conditions over time may encourage assemblage partitioning among differential instream habitats, 2) past-landscape disturbances may have greater influence on current instream habitats and fish assemblage structure, 3) weak relationships between catchment land cover and instream habitats may be common in low elevation regions, and 4) seasonal hydrologic patterns may dominantly influence instream habitat conditions and fish assemblage structure. This study adds essential information towards a better understanding of how South Atlantic coastal plain fish assemblages respond to abiotic factors across multiple spatial scales. Such knowledge will help improve management and conservation strategies, as well as assist in the development of appropriate indicators for standardized evaluations of ecological integrity.

Introduction

A key prerequisite for the conservation of biodiversity, particularly in under-surveyed systems, is to determine the number and types of communities that exist; such efforts provide a starting point for researchers to assess status, trends, and losses over time (Angermeier and Winston 1999). Further identifying the primary environmental factors that influence community composition, and the relevant spatial scales at which they manifest, is a particularly important component in the development of appropriate

conservation and management plans (Allan 2004; Fausch et al. 2002; Johnson and Host 2010). Hierarchical theory provides a framework for identifying the multi-scale factors that shape fish assemblages, where at fine scales fish assemblages are structured according to local abiotic factors such as hydrologic regimes, physiochemical gradients, and instream habitat availability, that are in turn constrained by increasingly larger scale catchment and landscape-level features which vary across physiographic and drainage boundaries (Frissell et al. 1986; Karr 1991; Townsend 1996). Variation at each scale contributes to unique differences in assemblage composition. Understanding the multi-scale influences on fish assemblages provides conservation managers with baseline information about how aquatic species composition varies naturally across the landscape, thereby helping them specify how anthropogenic activities alter expected fish assemblage structure.

South Atlantic coastal plain streams are unique and under-studied freshwater systems that provide crucial habitats for a wide range of aquatic taxa including many endemic habitat specialists. In South Carolina, coastal plain streams provide crucial habitats for N=26 endemic lowland specialist fish species (Rohde et al. 2009), as well as a wide variety of mussels (N=27; Bogan and Alderman 2008) and crayfish (N=26; Arnold Eversole, *pers comm.*). Coastal plain streams are typified by relatively harsh environmental conditions, with pronounced natural seasonal variation in flow regimes, and frequent exposure to extreme weather patterns (e.g., drought, tropical storms). In contrast to higher-elevation upland streams which have relatively uniform stream channel and hydrologic features (single channel with flow), low-elevation coastal plain stream

channels tend to be poorly defined and vary greatly across topographical gradients, ranging from confined channels with flow, to braided/swampy low-flow systems. Such seasonal variability and diversity in coastal stream habitats has forged, over time, a unique community of coastal plain fauna and associated life history adaptations. However, the identification of coastal plain fish assemblage types, their spatial variation, and the multi-scale abiotic influences that shape them are poorly documented and understood in the South Atlantic coastal plain.

Several previous studies of coastal plain fish assemblages have emphasized the importance of instream habitat features, particularly large wood (Benke et al. 1985; Crook and Robertson 1999; Sheldon and Meffe 1995), stream size (Paller 1994), and hydrological flow gradients (Adams et al. 2004; McCargo and Peterson 2010; Meffe and Sheldon 1988) as drivers of assemblage structure. Yet little has been published that explicitly examines the influences of abiotic factors across multiple spatial scales on coastal plain fish assemblages. Researchers have conducted multi-scale analyses of the environmental influences on fish assemblages in many other geographic regions, and conclusions regarding the relative importance of various instream and landscape-level abiotic influences have yielded inconsistent results, indicating that the scales at which abiotic factors influence fish assemblages vary across different physiographic regions and stressor gradients (Esselman and Allan 2010; Hoeinghaus et al. 2007; Johnson et al. 2007; Wang et al. 2006). Such incongruous results indicate the need for multi-scale analyses unique to the geographic area of conservation interest, particularly in understudied aquatic systems. A better understanding of how fish assemblages respond to

abiotic factors across spatial scales will help improve management and conservation strategies, as well as assist in the development of appropriate indicators for standardized evaluations of ecological integrity. Previous attempts to develop and implement evaluations of ecological integrity in this region have been restricted to the upper coastal plain (Paller et al. 1996), a narrow higher-elevation region which lacks the overall diversity of stream habitats observed in the lower-elevations of the South Carolina coastal plain. An effort to implement a coastal plain based Index of Biotic Integrity (IBI) by a neighboring state yielded counter-intuitive results, where proposed metrics reflecting positive aspects of community health correlated negatively to a habitat quality index (Patti Lanford, GA Dept. of Natural Resources, *Pers. Comm.*), exemplifying the complexity of this region and further indicating the need for a better understanding of South Atlantic coastal plain fish assemblages and the multi-scale abiotic factors that influence them.

Here, we 1) describe the taxonomic patterns in fish assemblages across South Carolina's coastal plain, and 2) develop statistical models to identify the dominant abiotic environmental factors that influence assemblage structure and the relevant spatial scales at which they manifest. The broad spatial extent of this study provides an opportunity to examine environmental influences at multiple scales across a range of stream types found in the South Atlantic coastal plain. Our results are intended to provide essential information to assist in the development of aquatic management and conservation strategies, and the development of aquatic integrity indicators.

Study Site

South Carolina is located in the Southern Atlantic region of the United States. We focused on 208 wadeable freshwater streams in South Carolina's coastal plain, a 45,773 km² area which includes four major drainage basins (Pee Dee, Lower Santee, Ashepoo-Combahee-Edisto (ACE), Savannah), and three Level IV ecoregions (Sand Hills, Atlantic Southern Loam Plains, Carolina Flatwoods (Figure 1.1; Omernik 1987). Streams located within the Level IV ecoregion Sea Islands/Coastal Marsh were excluded due to predominant estuarine influences. Elevations of this region range from approximately 90m in the Sand Hills to nearly sea level at the coastal zone boundary. Rainfall averages 127-132 cm/yr (www.dnr.sc.gov/climate), with highest average rainfall during the winter/spring and lowest annual rainfall during summer months. There were incipient to moderate drought conditions throughout our summer sample periods (2006-2011), excluding 2009 which exhibited normal summer rainfall. Mean daily maximum temperatures range from 17°C in the winter months to 32°C in the summer months. Predominant land cover disturbances in the region range from tobacco, soybean and corn row-crop agriculture in the northern region (Pee Dee drainage), to rotating evergreen silvicultural crops in the southern portion (ACE/Savannah drainages; Kohlsaet et al. 2005). Streams of this region generally have poorly defined channels, are low gradient and often blackwater, have low flows, are naturally low in pH, alkalinity, conductivity, and dissolved oxygen, have a shifting sand and/or organic debris substrate, and are generally less productive in both their abundance of fish and macroinvertebrates than their upland counterparts (Smock et al. 1985). Many of the sampled streams had been

channelized or altered in the past for irrigation, transport of goods, or to promote areas of soil drainage for agricultural, silvicultural, or other anthropogenic purposes (Kapsch 2010).

Methods

Sample Locations

Data for this study are a subset of a larger evaluation of statewide aquatic resources conducted by the South Carolina Department of Natural Resources (SCDNR) in 2006-2011, termed the South Carolina Stream Assessment (SCSA). Statewide sample locations were randomly selected from a probabilistic framework designed by the South Carolina Department of Natural Resources, described in detail elsewhere (Scott 2008). Sample reaches were selected with known probability using a multistage design from a list frame of all stream segments in the state, stratified by ecobasin (unique combination of EPA level IV ecobasin and major drainage basin) and stream size, and allocated proportionally among ecobasin strata to allow statistically defensible estimates of statewide resource parameters from the sample data. Sample locations drained catchments ranging from 0.17 to 154.13 km² were selected to share no more than half of the drainage area of any downstream site, as a means of maintaining independence among samples. Selected stream reaches were either single channels, or minimally braided to ensure a comprehensive fish sample.

Fish Collection

We collected fishes from 208 sample locations with backpack electrofishers (Appalachian Aquatics Model AA-24) from spring to fall in the years 2006-2011 during

base flow conditions. Sample methods followed standard protocols employed by the South Carolina Department of Natural Resources for sampling fish in wadeable streams (Scott et al. 2009). This protocol dictates a three-pass electrofishing method along a stream reach length equivalent to 20x average width (reach length range 100-200 m, median = 100 m). Block nets were utilized at both ends of the sample reach unless the reach was sufficiently blocked at one (or both) ends by a natural barrier. All fishes were collected with dip nets (4.8-mm mesh), field identified and enumerated, and released upon sample completion. Specimens that could not be positively identified in the field were preserved in a 90% ethanol solution and returned to the lab for positive identification. Voucher specimens of all species were either preserved or photographed.

Instream Parameters

We quantified a range of in-stream parameters for each sample reach at the time of sample (Table 1.1). Stream channel width measurements were taken at the 0, 25, 50, 75, and 100m distances along each sample reach and averaged to obtain mean stream width. Physical and chemical data, including water temperature, dissolved oxygen, conductivity, and pH were recorded prior to fish sampling using a YSI 556 MPSTM multiparameter probe. Turbidity was recorded using a MicroTPWTM turbidimeter. Depth, velocity, and substrate measurements were quantified using the ‘zig-zag’ habitat sampling method after the completion of fish sampling (Bevenger and King 1995; Scott et al. 2009). This method required traversing a random ‘zig-zag’ longitudinal transect in a downstream to upstream direction along the sample reach, recording depth, velocity, and substrate at 50 randomly selected locations. Inorganic substrate particles were

measured in millimeters at the intermediate axis and median particle size was calculated for each site. The vast majority of coastal plain streams contained a median particle size of <2mm, therefore we examined inorganic substrates as percent sand in all statistical analyses. Organic substrates were classified into one of the following percent categories: 1) fine particulate organic matter (FPOM), 2) coarse particulate organic matter (CPOM), 3) fine woody debris (FWD), 4) large woody debris (LWD), and 5) aquatic vegetation (AV; Scott et al. 2009). If one of the 50 random sampling points fell on a dry section of the stream (discontinuous flow), that measurement was recorded as 'dry' and the total of 50 measurements was reduced by the number of 'dry' points. Site elevations were obtained in the lab from Terrain Navigator Pro Version 9.2 (Trimble Navigation Limited, Sunnyvale, CA, USA) using the North American Datum 1983 map layer.

Two person crews conducted geomorphological surveys at sample locations during the winter succeeding the fish sample. Surveying techniques followed those described by Harrelson et al. (1994). Slope measurements were performed from head of riffle to head of riffle (where possible), or along stable runs and were approximately 90m in length. Crews measured a single representative cross-section of the sampled reach, at either riffle areas or stable run areas when riffles were not present. We extracted geomorphological parameters from the cross-sectional data using RIVERMorph® software (Table 1.1). We set bankfull stage at top of bank, thereby defining bankfull as the elevation of the floodplain adjacent to the active channel. We categorized sinuosity as a binary variable, describing each stream as either sinuous or not sinuous. Additionally, we qualitatively classified the general geomorphological character of each stream as

either a) not channelized with distinct single channel, b) channelized, or c) not channelized with swamp-like and braided characteristics (Type Code; Table 1.1).

Catchment Land Cover and Stream Network Parameters

We quantified land cover within study catchments and 120m riparian buffers using ArcGIS® 10.0 (Table 1.1). We mosaicked a combination of the highest resolution available digital elevation models (DEMs) for the South Carolina coastal plain, which included light detection and ranging data (3m resolution LiDAR; SCDNR Technology Development Program), and 10m-30m resolution data obtained from the US Geological Survey (Fry et al. 2011). We used Arc Hydro v2.0 to define stream networks based on a 1.00 km² catchment threshold definition. Delineated catchments included the entire drainage area upstream of sample locations, and riparian buffers included 120m land areas adjacent to defined stream networks within catchments. We extracted National Land Cover Data (NLCD) classes for 2006 for each catchment and associated 120m riparian buffer (Gesch et al. 2002). The NLCD distinguishes 20 land cover class designations for 2006, which we initially combined into 6 land cover categories according to (Fry et al. 2009). Forest land cover was further sub-categorized as either deciduous/mixed (NLCD2006 classes: 41, 43) or evergreen (NLCD2006 class: 42) (Table 1.1). All map layers were projected in the Universal Transverse Mercator (UTM) projection system (zone 17 N), using the North American 1983 datum.

We additionally calculated several stream network attributes which may influence species composition at a given sample location via dispersal opportunity and community connectivity (Table 1.1; Brown et al. 2011; Leibold et al. 2004). We used our created

stream networks to determine the dendritic distance from sample locations to their corresponding downstream HUC 8 mainstem river. We then quantified separate upstream and downstream mainstem network attributes including number of dams (USACE 2013), number of impoundments (NHD; USGS 2011), number of road crossings (NHD; USGS 2011), and number of tributaries (defined stream network).

Data Analysis

We performed a hierarchical agglomerative cluster analysis using the Wards linkage algorithm on a fish density matrix (number of individuals per 100m²) to identify groups of species that commonly co-occur in coastal plain wadeable streams. A $\log_{10}(x+1)$ transformation was performed on the species density matrix to reduce the effect of large differences in fish densities among sample localities. The Euclidean distance measure was utilized to calculate species similarity. Preliminary analysis of the full species matrix of 77 species revealed an inordinate influence of several rare species (Lohr and Fausch 1997). Twenty-nine species whose densities were represented in $\leq 2\%$ of sites were identified as strongly influencing the analysis based on rarity alone, and were subsequently omitted from the analysis. The vast majority of these rare species were considered to be ‘upland’ species, whose distributions do not fully extend into South Carolina’s coastal plain, but were captured at very low densities in the Sand Hills ecotone. We also detected a strong influence of *Gambusia holbrooki* based on its ubiquitous presence and extreme variability in densities among sites. The variability of this species obscured the underlying fish assemblage structure and it was omitted from all subsequent analyses (Lohr and Fausch 1997; Matthews and Marsh-Matthews 2011). The

final data matrix contained 48 species; the cluster analysis was conducted using the cluster package of the R 2.15.3 statistical software (R Core Development Team 2012).

We used an indicator species analysis to assist in describing the faunal composition of each classification group (i.e. fish assemblage) and to identify the appropriate number of groups for use in subsequent analyses (Dufrêne and Legendre 1997). The indicator species analysis was conducted using the labdsv package in R statistical software (R Core Development Team 2012). Two- to four- group solutions were explored by calculating the indicator value (I_v) of each species for each group. A perfect indicator species ($I_v=100$) would be found if a species occurred in one group and in no other groups (McCune and Grace 2002). The significance ($\alpha = 0.05$) of each indicator species was determined by 999 Monte-Carlo permutations. A four- group solution was selected for further analysis because it had the highest number of significant indicator species, providing evidence of greater difference among assemblages.

We used non-metric multidimensional scaling (NMDS) to provide further validation and insight into the underlying structure of the four fish assemblages defined by the cluster analysis (Clarke 1993; Kruskal 1964). NMDS was performed in R's vegan package (R Core Development Team 2012) using the Bray-Curtis distance measure (Bray and Curtis 1957), a random starting configuration, and 1000 runs with real data. We used a Monte-Carlo test with twenty iterations and ten randomized runs to determine the probability of obtaining an equal or lower stress value by chance ($\alpha=0.05$). From the NMDS output, we produced plots showing species coded by their respective cluster group membership to further visualize and verify the cluster analysis outcome.

We used classification random forests (RF) analysis to identify the multi-scale abiotic variables that best distinguish among the four coastal plain fish assemblages determined by the cluster analysis (Breiman 2001; Cutler et al. 2007). Machine learning techniques such as RF provide an alternative modeling paradigm to traditional statistics, where no a priori model is defined, and complex data structures (i.e., non-normal distributions, interactions) are accommodated. Machine learning techniques use an algorithm to learn the relationship between the response and its predictors by identifying dominant patterns in the dataset (Breiman 2001; Elith et al. 2008). RF represent an advance in machine learning techniques that have increased the accuracy and prediction power of single classification and regression trees by the creation of an ensemble of trees (Breiman 2001). RF are non-parametric, can handle both categorical and continuous data as either predictor and/or response variables, can handle high-order interactions, are insensitive to outliers, and can accommodate missing data by using surrogates (Breiman 2001; De'ath and Fabricius 2000; Urban 2002). Categorical RF fit an ensemble of trees to a dataset, where each individual tree in the forest is built using a randomly selected bootstrap sample of the training dataset. In addition, only a random subset of predictor variables is considered for node and splitpoint selection (Amit and Geman 1997). In this way, two elements of randomness are injected into the procedure. Observations not included in the bootstrap samples are passed down their respective trees, and each tree's terminal nodes contain a predicted categorical response to different combinations of observed values among predictor variable pathways. Each tree has a 'vote' in the most important predictive variables to split on, and on the categorical responses of different

values of input combinations; and the majority of votes among the ensemble of trees (i.e. forest) ‘wins’. Therefore, we can a) predict and rank variables that most strongly influence an outcome (variable importance plot), and b) visualize functional relationships by examining responses of individual predictors on the outcome, while holding the effect of all other predictive variables constant (partial dependence plots).

RF modeling was conducted by building 5000 trees using default values for other parameters in the randomForest package in the R programming environment (R Core Development Team 2012). RF models have known biases in variable importance selection for highly correlated predictor variables; therefore we conducted a preliminary screening of our abiotic variables to eliminate highly correlated variables (Strobl et al. 2007). Riparian land cover proportions were highly correlated with whole catchment proportions (all $r > 0.80$), average velocity was highly correlated with standard deviation of velocity ($r = 0.89$), average depth was highly correlated with the standard deviation of depth ($r = 0.70$), downstream dams were highly correlated with downstream impoundments and downstream tributaries (all $r > 0.70$), upstream dams were highly correlated with upstream impoundments ($r = 0.71$), and upstream impoundments were highly correlated with watershed area ($r = 0.72$). Therefore, riparian land cover variables, the standard deviation of velocity, average depth, downstream dams and impoundments, downstream and upstream tributaries, and upstream impoundments were eliminated from further model development. We further eliminated the lowest ranking predictor variables that did not contribute to model importance including fine particulate organic matter, downstream roads, slope, and % catchment open water.

The RF algorithm builds trees based on repeated randomized samples of the dataset, therefore it is not essential to hold back data for testing after model creation to obtain an unbiased estimate of error. Model performance was evaluated with three accuracy measures calculated using the resubstitution method (Theodoridis and Kourtroubas 2009). The three measures were the Proportion Correctly Classified (PCC), Cohen's weighted Kappa statistic (weighted κ), and the area under the receiver operating curve (Gauch 1982). Both PCC and weighted κ are derived from the model confusion matrix, which gives the actual versus predicted classifications of group membership. PCC performance measures are given in two forms: 1) an overall PCC percentage (accuracy) representing the total number of correctly classified cases divided by the total number of cases across all outcome classes, and 2) a measure of accuracy for a specific outcome class (precision). Weighted κ corrects the PCC for agreement caused by chance, and gives a value ranging from -1 to 1 (Cohen 1968). A positive value indicates greater agreement between modeled and measured classifications than expected by chance alone, and a negative value indicates less agreement than expected by chance alone. Cohen's weighted κ was calculated using the vcd package in R (R Core Development Team 2012). The AUC is derived from plotting the true positive rate (sensitivity) against the false positive rate (specificity), with each point plotted representing a sensitivity/specificity pair. The area under the resulting plot is a measure of how well the model correctly classifies groups. AUC values range from 0 to 1, with values > 0.5 indicating better model performance than expected by chance alone (Swets

1988). We used the ordROC function in the nonbinROC R package in R to calculate AUC values (<http://cran.r-project.org/web/packages/nonbinROC/index.html>).

Lastly, we performed a principal components analysis on our multi-scale abiotic predictor variables (instream, land cover, and stream network parameters) using the vegan package of R (R Core Development Team 2012). This analysis was intended to show relationships among abiotic predictor variables, and further aid in the interpretation of RF results. Principal components analysis (PCA) is used to reduce the dimensionality of data, and to transform correlated variables into significant, independent components that help us better visualize and understand interdependencies among variables. Variables were first scaled and centered, and the PCA was performed on the correlation matrix (Legendre and Legendre 1998).

Results

Cluster and Indicator Species Analyses

Four predominant coastal plain fish assemblage groups were identified with hierarchical cluster analysis, and described by an indicator species analysis. The indicator species analysis found thirty-nine species as significant at the $\alpha = 0.05$ level, and membership was partitioned accordingly into the four fish assemblage groups (Table 1.2). We assigned names to each of the four fish assemblages based on the prevailing taxonomic and/or ecological attributes of the species with the highest indicator values for each group. Group one was named the fluvial assemblage (n=12 species), since flow is a primary ecological requirement for all of its constituents (Rohde et al. 2009). The fluvial assemblage contained shiners, darters, madtoms, and bullheads. Only three members of

the fluvial assemblage are completely restricted to the South Carolina coastal plain (*Pteronotropis stonei*, *Etheostoma fricksium*, *Opsopoeodus emiliae*); most of the identified species had ranges extending into higher elevation regions. Several members of the fluvial assemblage are only found in the Savannah, ACE, and Lower Santee basins (*Percina nigrofasciata*, *Noturus leptacanthus*, *Notropis lutipinnis*, *Opsopoeodus emiliae*, *Etheostoma fricksium*), and are absent from the Pee Dee system. All members of the fluvial assemblage are considered to be dependent on flow and specific benthic substrates (Rohde et al. 2009) for either all or part of their life cycle, and are generally intolerant to stream drying.

Group 2 was named the eastern mudminnow assemblage (n=1 species), since *Umbra pygmaea* was the sole constituent. The eastern mudminnow is restricted to the South Carolina coastal plain, and is typically found over coarse organic substrates in small headwater backwater streams with little to no flow (Rohde et al. 2009). The eastern mudminnow is very tolerant to both low pH and low dissolved oxygen conditions, and has specific adaptations to stream drying including the capability of gulping atmospheric air using a physostomous swim bladder, and the ability to aestivate in moist soils.

Group 3 was named the centrarchid assemblage (n=10 species); several cosmopolitan centrarchids dominated this group including *Lepomis auritus*, *Lepomis macrochirus*, *Lepomis punctatus*, and *Micropterus salmoides*. This group also included *Anguilla rostrata*. Only three members of the centrarchid assemblage were restricted to the South Carolina coastal plain in our study (*Lepomis punctatus*, *Anguilla rostrata*, *Labidesthes sicculus*), all other members ranged into higher elevations. All assemblage

members are habitat generalists and opportunistic feeders. Several species in this group are long lived and can obtain fairly large sizes and therefore may prefer fairly stable large stream habitats with some flow and depth variability.

Group 4 was named the non-fluvial assemblage (n=16 species), since all of its members either thrive in or require aquatic environments with little to no flow (Rohde et al. 2009). Nine members of the non-fluvial assemblage are either mostly or entirely restricted to the South Carolina coastal plain (*Centrarchus macropterus*, *Enneacanthus gloriosus*, *Aphredoderus sayanus*, *Acantharchus pomotis*, *Lepomis marginatus*, *Enneacanthus obesus*, *Elassoma zonatum*, *Amia calva*, *Etheostoma fusiforme*). All of the non-fluvial species are commonly found over coarse organic and muck substrates in streams with low to no flow. The non-fluvial assemblage contains species that are tolerant to high turbidity and stream temperatures (*Notemigonus crysoleucas*), low pH (*Enneacanthus obesus*), and low dissolved oxygen conditions (*Amia calva*, *Etheostoma fusiforme*).

Non-Metric Multidimensional Scaling

The NMDS resulted in a 3-dimensional solution with a final stress value of 16.64, and a Monte Carlo test indicated significance at $p < 0.001$. To highlight the similarity between the NMDS ordination and the cluster analysis assemblage groups, we plotted species in a 3-dimensional ordination space and coded each species to show their respective fish assemblage association as determined by the cluster analysis (Figure 1.2). The NMDS reiterated and validated the cluster analysis findings, highlighting the separation of four assemblages of coastal plain fish species. The NMDS also showed that

fish assemblage groups are not entirely distinct, but overlap to some degree. Species classified as belonging to the fluvial and centrarchid assemblages overlapped to some extent among samples, likewise species classified as belonging to the centrarchid and non-fluvial assemblages overlapped. However, species classified as belonging to the fluvial and non-fluvial assemblages displayed no overlap, and the eastern mudminnow assemblage was distinct from all other assemblages.

Random Forests

The RF model correctly classified the prevailing fish assemblage found in 60.84% of our sample sites, and performed better than chance alone ($AUC = 0.74$). The weighted kappa statistic indicated a moderate strength of agreement between observed and predicted values (weighted $\kappa = 0.46$). An examination of individual class accuracies (precision) from the output confusion matrix provided additional information on model performance. The fluvial assemblage had the highest class precision at 84.78%. The eastern mudminnow and non-fluvial assemblages had class precisions of 54.72% and 68.75% respectively. The centrarchid assemblage had the lowest precision (39.13%), with misclassifications most commonly placed in the non-fluvial assemblage.

Variables associated with geographic gradients (ecobasin) and instream parameters (velocity, channel form, stream size, and depth) were the most important classifiers in our model (Figure 1.3). Our variable importance result additionally indicated that land cover played a diminished role in predicting assemblage group membership in comparison to geographic gradients and instream parameters. There was

no indication that the RF model was biased against selecting categorical variables; ‘Ecobasin’ and ‘Type Code’ ranked high in importance (Strobl et al. 2007).

Partial dependence plots isolate and examine the behavior of individual predictors on the outcome while holding the effect of all other predictive variables constant. We provide partial dependence plots for the top eleven most important predictor variables. The most influential predictor, ecobasin, is presented as a series of ecobasin maps (one per fish assemblage) that show shaded areas indicating high, medium, and low classification probabilities (Figure 1.4). The ecobasin partial dependence plot predicted fluvial and centrarchid assemblage classification to be the greatest in the inner coastal plain, particularly the inner ACE basin; however the centrarchid assemblage classification was predicted to range into lower elevation ecobasins, particularly in the Lower Santee. In contrast, the eastern mudminnow and non-fluvial assemblage classifications were predicted to be most probable in the outer coastal plain, with the non-fluvial assemblage probability of classification predicted to be greater in the Pee Dee and Savannah ecobasins than in the ACE or Lower Santee.

Partial dependence plots showed that the fluvial and centrarchid assemblage classification probabilities increase with increased average velocities, increased average wetted width, increased dissolved oxygen, increased watershed area, and increased width of bankfull (Figures 1.5a, 1.5c, 1.5e, 1.5f, 1.5j). However, the fluvial assemblage had a higher probability of classification in non-channelized single channel streams, whereas the centrarchid assemblage did not show a clear association with stream channel types (Figure 1.5b). The fluvial and centrarchid assemblages further differed in that the

probability of fluvial assemblage classification was positively associated with increased elevation, while the centrarchid assemblage was not associated with elevation (Figure 1.5d). Likewise, the probability of fluvial assemblage classification was negatively associated with increased depth diversity, while the probability of centrarchid assemblage classification was positively associated (Figure 1.5g). Also, the probability of fluvial assemblage classification was positively associated with deciduous/mixed forest land cover and large wood, while the centrarchid assemblage was negatively associated (Figures 1.5h, 1.5i).

Partial dependence plots showed that the probability of eastern mudminnow and non-fluvial assemblage classification were both negatively associated with average velocity, average wetted width, elevation, dissolved oxygen, and watershed area (Figures 1.5a, 1.5c, 1.5d, 1.5e, 1.5f). The eastern mudminnow assemblage had a probability of classification across channel types, but showed an affinity for channelized and non-channelized swamp-like and braided streams (Figure 1.5b). In contrast, the non-fluvial assemblage was predicted to be most probable in only channelized and non-channelized swamp-like and braided streams. The eastern mudminnow and non-fluvial assemblages further differed in that the probability of eastern mudminnow assemblage classification was negatively associated with depth diversity, large wood, and width of bankfull, while the probability of non-fluvial assemblage classification was positively associated (Figures 1.5g, 1.5h, 1.5j). Likewise, the probability of eastern mudminnow assemblage classification was positively associated with deciduous forest catchment land cover, while the non-fluvial assemblage was negatively associated (Figure 1.5i).

Principal Components Analysis of Multi-scale Abiotic Parameters

We conducted a PCA to help us better understand and visualize the interdependencies among predictor variables. The first two PCA axes accounted for 21.17% and 11.93% of the total variance respectively, and 33.10% cumulatively (Figure 1.6). Axis 1 represented a gradient in stream hydrology, where sites with increased average velocity were positively associated with increased dissolved oxygen, elevation, average stream width, watershed area, deciduous/mixed forest land cover, and large wood, and negatively associated with catchment wetland land cover, turbidity, fine wood, and coarse particulate organic matter. Axis 2 represented a land cover disturbance gradient, contrasting the environmental conditions of two land disturbances - agrarian and evergreen forest land cover (i.e., silviculture). We considered evergreen forest to be a disturbance land cover because South Carolina's coastal plain evergreen forests are dominantly comprised of pine species in silvicultural systems, and it is estimated that natural pine cover (i.e. longleaf) has been severely reduced to less than 4% of its historic coverage (Kleppel et al. 2007; USDA 2011). Axis 2 showed that agrarian (and to a lesser extent, urban) catchments were positively associated with increased pH, conductivity, and width and depth of bankfull, and sand substrates, and negatively associated with evergreen land cover (silviculture).

Discussion

Though many species are ubiquitous throughout the South Carolina coastal plain (e.g., redbfin pickerel, pirate perch), we identified four fish assemblages comprised of commonly co-occurring species that were more or less distinctive. No species operated as

a perfect indicator of any assemblage (i.e. found only in sample localities classified as a certain assemblage and not others), highlighting the propensity of lowland streams to commonly share species (Warren et al. 2000). Such overlap may partially reflect historic connectivity among drainages, or ecological convergence due to the high degree of environmental fluctuation, or the environmental harshness that is present in the coastal plain (Chesson and Huntly 1997; Hocutt et al. 1986; Hubbell and Foster 1986). Regardless, a generalized pattern emerged indicating that fluvial and/or centrarchid assemblages were found in coastal plain streams that maintain flow, and eastern mudminnow and/or non-fluvial assemblages were found in streams with reduced or absent flow.

The four coastal plain fish assemblages differed according to natural gradients in the underlying stream habitat template, primarily diverging across natural geographic gradients (ecobasin) and instream parameters (velocity, channel form, stream size, and depth). Our RF model predicted fluvial assemblages to be most probable in the higher elevations of the upper coastal plain, with generally higher probabilities in the ACE basin than the Pee Dee basin. Fluvial assemblages were most probable in large, high-velocity, relatively shallow non-channelized single channel streams with large wood substrates and increased catchment forest cover. Centrarchid assemblages were also predicted to be most probable in large high velocity streams, however differed in that this assemblage was more probable in a variety of ecobasins across elevations, in both channelized and non-channelized deep streams, with decreased amounts of large wood substrates and catchment forest cover. Differences in fluvial and centrarchid assemblage habitats may,

in part, be explained by species turnover with longitudinal changes in stream environments (Paller 1994). In contrast, the eastern mudminnow assemblage was predicted to be most probable across the lower elevation coastal plain in small, shallow, low-velocity, channelized and swamp-like streams with decreased amounts of large wood, increased forest cover, and decreased width of bankfull (headwater streams). Non-fluvial assemblages were also predicted to be most probable in the lower elevation coastal plain, however were predicted to be more probable in Pee Dee and Savannah ecobasins than in ACE or lower Santee ecobasins. The non-fluvial assemblage also differed from the eastern mudminnow assemblage in that it was found to be more probable in deeper streams with increased large wood substrates, with decreased amounts of large wood and increased widths of bankfull (non-headwater streams).

Influence of Instream and Catchment parameters on Assemblage Composition

Natural geographic gradients (ecobasin) and instream parameters associated with velocity, channel form, stream size, and depth played a greater role in distinguishing fish assemblages than catchment land cover and stream network parameters. Additionally, our PCA results showed that the abiotic factors our RF model ranked most influential in predicting assemblage membership (average velocity, average width, elevation, dissolved oxygen, watershed area, depth diversity) were uncorrelated with an anthropogenic (evergreen/agriculture) land cover disturbance gradient (Figure 1.6). This may indicate that coastal plain fish assemblages and instream conditions vary across natural environmental gradients that operate independently from an anthropogenic land cover disturbance gradient.

We propose four possible explanations as to why geographic gradients and instream parameters have greater explanatory power than catchment land cover parameters in determining coastal plain fish assemblage composition, and why instream factors may not be strongly linked to land cover factors. First, previous studies evaluating multi-scale influences on stream fish assemblages have shown that instream environmental factors have greater explanatory power than land cover factors in largely undisturbed catchments (Lyons 1996; Wang et al. 2006; Wang et al. 2003; Wiens 2002). Support for this finding resides in theories of hierarchical organization of stream systems, where in relatively undisturbed landscapes, there exists a dynamic equilibrium among catchment, riparian, and instream conditions. This dynamic equilibrium creates a relatively stable instream habitat template that constrains species life history strategies and determines the composition of biological communities (Allan 2004). As anthropogenic landscape influences increase past some intensity threshold, this equilibrium among catchment, riparian, and instream conditions is broken, and instream conditions reestablish new equilibria with their environments over time. Hence, the condition and structure of fish assemblages tends to reflect the altered instream environments (e.g., altered flow patterns, pollutant pulses, increased sedimentation, temperature extremes) associated with the cumulative effects of anthropogenic landscape degradation. Current landscape disturbances in our sampled catchments were generally not intense; the vast majority (n=185, 89% of total sites) of catchments contained <10% urban land cover, approximately half (n=100) of our catchments contained <20% agrarian land cover and none had >70%, and only 15 sites had catchments with greater

than 50% evergreen (silviculture) forest cover (Wang et al. 2006). Our randomized sampling regime likely captured the average gradient of anthropogenic landscape intensities throughout the coastal plain, rather than anthropogenic land use disturbance extremes. If current coastal plain landscape disturbances are not intense, and we assume that current instream and biological conditions reflect current landscape conditions, then we can postulate that local instream factors should show greater explanatory power than land cover factors.

Second, despite the fact that we observed relatively non-intense catchment anthropogenic disturbances, past coastal landscape disturbances are known to have been severe. Therefore, the postulation that coastal plain fish assemblages show weak relationships with catchment land cover because streams have maintained a dynamic equilibrium among catchment, riparian, and instream conditions over time is likely flawed. Extensive deforestation and agriculture operations pervaded the South Atlantic coastal landscape throughout the 18th and 19th centuries; such land conversions reached their peak in the 1920s when nearly all timber had been extracted, and row-crop farm parcels sized 100-500 acres pervaded the region (Beck et al. 2012; Phillips 1994). Concurrently, South Carolina was the preeminent leader in infrastructure improvements from the 1790s to the 1830s, and developed an extensive system of more than 2000 miles of canals and ditches for agricultural expansions and increased connectivity with the port of Charleston (Kapsch 2010). While we cannot directly account for these past landscape disturbances, it is likely that they had unintended, and in some cases irreversible impacts (e.g. ditching, sedimentation) on coastal plain streams and fish assemblages. In recent

decades, the South Atlantic coastal plain has generally transitioned away from agrarian land to unutilized grass/shrubland, planted pine, and to a lesser extent, urban land use (Ainslie 2002; Fry et al. 2009). Current land cover conditions observed in our study may not reflect past landscape disturbances and their impacts on instream environments. It follows that current stream conditions may be more tightly linked to past landscape conditions rather than current landscape conditions, thus we would expect to observe stronger relationships between instream factors and fish assemblages, and weaker relationships between current land cover and fish assemblages (Harding et al. 1998; Wang et al. 2001).

Third, instream conditions may be weakly related to catchment land cover conditions in low elevation regions. Our stream sample locations were predominantly located in low elevation areas (median elevation = 32.6m) with low localized topographic variation within catchments, resulting in naturally low overland runoff and erosion rates and poorly defined drainage patterns (McNab et al. 2007). Many of the stream-degrading processes associated with landscape disturbances that we observe in higher-elevation regions result from increased overland flows across higher-gradient catchments, such as increased sediment transport, flash flooding, stream channel incision and erosion, nutrient and pollution pulses, etc. (Paul and Meyer 2001). Such characteristic responses of streams to landscape disturbances may be weak in coastal plain catchments due to the low-gradient and low topographical variation inherent to the coastal plain. As a result, we might expect local instream conditions to operate more independently of the dominant

land cover of the local landscape in which it resides, and therefore instream conditions may supersede the influence of land cover conditions on assemblage structure.

Fourth, we may have failed to capture strong evidence of land cover-instream linkages due to the mono-seasonal nature of our sampling regime. All of our samples occurred in warm-weather months (April – September), during periods of stream drying. Additionally, the South Atlantic coastal plain experienced conditions of incipient to moderate drought during our summer sample period of 2006-2011, excluding 2009 which exhibited normal summer rainfall (SCDNR: www.dnr.sc.gov/climate). South Carolina coastal plain streams typically exhibit a fairly predictable seasonal variation in flow, with high flows during the wet cool winter months, and low flows and stream drying during the warm, dry summer months (Kohlsaet et al. 2005). However, seasonal flow dynamics among streams may be influenced by and differ across various land cover conditions. For example, streams in disturbed landscapes may show less dynamic flow regimes across seasons than streams in undisturbed landscapes. We failed to capture such seasonal dynamics in our sampling regime, and therefore cannot comment extensively about compositional changes across seasons. However, we do know that coastal plain fishes are adapted to maximize reproductive capacity and survival in variable hydrological environments (Poff 1996). The composition and structure of coastal fish assemblages, therefore, may be largely driven by dispersal dynamics according to seasonal variation in stream flows (Falke and Fausch 2010; Leibold et al. 2004; Schlosser and Angermeier 1995). As streams begin to dry in the summer months, fishes that require flow may migrate away from spawning or other habitats to summer refugia areas that maintain

flow. Fishes better suited to deal with harsh environmental conditions may remain, or move to stream reaches of increased size (pools). When flows resume as winter approaches, dispersal among localities may increase as stream habitats diversify into flowing environments. In this manner, the influence of local environmental habitat conditions (e.g. stream size, velocity, dissolved oxygen) may be accentuated in summer months, and predominantly influence fish assemblages over land cover conditions. We suggest that future studies employ a cross-seasonal sampling strategy to further explore the seasonal dynamics of coastal plain fish assemblages within a variety of coastal plain stream environments.

Implications for Conservation Strategies

Our study provides insight into the potential obstacles faced by researchers attempting to discern aquatic integrity indicators or develop multi-metric indices of biological health (e.g., IBIs) for the South Atlantic coastal plain. Such indicator methods evaluate biological health as the degree of departure from undisturbed or expected biological conditions representative of healthy stream habitats of the region (Angermeier and Karr 1994; Davis 1995; Karr 1981). However, these types of assessment procedures may be difficult to implement in the South Atlantic coastal plain because there at least two natural undisturbed (reference) stream habitats co-occur across the coastal landscape (fluvial and non-fluvial streams), that contain very different fish assemblages. A fluvial/centrarchid assemblage is expected in streams that retain flow and its correlates; species within these assemblages likely reflect a quantifiable gradient in tolerance to harsh and/or degraded stream conditions (Rohde et al. 2009). In contrast, we expect a

non-fluvial / eastern mudminnow assemblage in streams with low to no flow, or that are in the process of seasonal drying; both of these assemblages are generally tolerant to harsh stream conditions. Each of the four fish assemblages shows adaptations to the variety of naturally occurring coastal plain stream environments, and none of the assemblages directly or clearly indicates a landscape-based anthropogenic disturbance.

Aquatic integrity indicators should be responsive to anthropogenic stresses and have limited sensitivity to natural variation (Karr 1991). Useful indicators display high sensitivity to a particular or suite of stressors, respond to stress in a predictable manner, reflect ecological changes, and have a known response to anthropogenic stress (Dale and Beyeler 2001). Our study shows that coastal plain fish assemblages predominantly vary across natural gradients, and are largely insensitive to anthropogenic land cover disturbances. These findings are important, because land managers and policy advisors cannot change the underlying natural features of the coastal plain environment, but can influence land cover activities and/or directly modify the local stream environment.

This study represents an evaluation of the multi-scale abiotic influences on fish assemblage structure in an understudied freshwater ecosystem. We recommend that researchers continue to explore South Atlantic coastal plain fish assemblage characteristics in novel and creative ways in order to identify the abiotic and biotic features of disturbed coastal plain fish assemblages and streams in further pursuit of how to best conserve the fish assemblages of this unique and diverse geographic region.

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Table 1.1.. Summary statistics for multi-scale abiotic predictor variables.

Abbreviation	Description	Median / Ecoregion	Mean	Range	Count
Elevation	Average watershed elevation (m)	32.6	39	0.9-139.6	
Velocity_M	Average velocity (m/s)	0.05	0.08	0-0.35	
Velocity_SD	Standard deviation of velocity (m/s)	0.06	0.06	0-0.24	
Depth_M	Average depth (m)	0.26	0.26	0.04-0.64	
Depth_SD	Standard deviation of depth (m/s)	0.12	0.13	0.03-0.32	
Width_M	Average width (m)	3.12	3.39	0.38-9.10	
AV	% Aquatic vegetation	0.02	0.08	0-0.96	
FPOM	% Fine particulate organic matter	0.02	0.07	0-1.00	
CPOM	% Coarse particulate organic matter	0.2	0.27	0-0.88	
FWD	% Fine wood	0.1	0.12	0-0.49	
LWD	% Large wood	0.1	0.12	0-0.40	
Sand	% Sand	0.26	0.27	0-0.80	
Temp	Temperature (°C)	22.56	21.73	8.98-33.34	
DO	Dissolved Oxygen (mg/L)	6.07	5.5	0.00-11.37	
Cond	Conductivity (µS/cm)	82	100	11-708	
pH	pH	6.67	6.64	4.92-8.33	
Turbidity	Turbidity (NTU)	5.47	9.45	1.03-59.29	
Slope	Slope	0	0	0-0.01	
Wbkf	Width at Bankfull (ft)	25.6	28.57	8.20-162.10	
Dbkf	Depth at Bankfull (ft)	1.8	2.22	0.30-8.00	
Sinuosity	Sinuosity (0=not sinuous, 1=sinuous)				0=67, 1=141
Type Code	Stream Type (1=not channelized single, 2=channelized, 3=not channelized multiple)				1=86, 2=66, 3=54
WS_Area	Watershed Area (km²)	20.71	30.63	0.17-154.13	
B_06_OPENWATER	% of 120m riparian buffer under open water cover	0	0.02	0-0.12	
B_06_URBAN	% of 120m riparian buffer under urban cover	0.03	0.05	0-0.58	
B_06_DECIDUOUS.MIXED	% of 120m riparian buffer under deciduous/mixed forest cover	0.01	0.05	0-0.62	
B_06_EVERGREEN	% of 120m riparian buffer under evergreen forest cover (silviculture)	0.18	0.19	0-0.68	
B_06_GRASSSHRUB	% of 120m riparian buffer under grass/shrub cover	0.11	0.12	0-0.40	
B_06_AGRICULTURE	% of 120m riparian buffer under agricultural cover	0.09	0.14	0-0.84	
B_06_WETLAND	% of 120m riparian buffer under wetland cover	0.42	0.43	0-0.90	
W_06_OPENWATER	% of catchment under open water	0	0	0-0.05	
W_06_URBAN	% of catchment under urban cover	0.05	0.07	0-0.48	
W_06_DECIDUOUS.MIXED	% of catchment under deciduous/mixed forest cover	0.02	0.05	0-0.39	
W_06_EVERGREEN	% of catchment under evergreen forest cover (silviculture)	0.23	0.26	0-0.80	
W_06_GRASSSHRUB	% of catchment under grass/shrub cover	0.15	0.17	0.03-0.52	
W_06_AGRICULTURE	% of catchment under agricultural cover	0.22	0.24	0.00-0.70	
W_06_WETLAND	% of catchment under wetland cover	0.18	0.2	0-0.61	

Table 1.1. continued. Summary statistics for multi-scale abiotic predictor variables.

Abbreviation	Description	Median / Ecoregion	Mean	Range	Count
DIST MS m	Distance to HUC 8 mainstem (m)	9778.5	10,967.95	323-36,031	
DS DAMS MS	Number of downstream dams on mainstem	0	0.26	0-5	
DS IMPOUND MS	Number of downstream impoundments on mainstem	0	0.43	0-4	
DS ROADS MS	Number of downstream roads on mainstem	3	3.13	0-12	
DS TRIBUTARIES	Number of downstream tributaries	3	4.23	0-33	
US DAMS MS	Number of upstream dams on mainstem	0	0.43	0-4	
US IMPOUND MS	Number of upstream impoundments on mainstem	0	0.74	0-8	
US ROADS MS	Number of upstream roads on mainstem	3	3.55	0-14	
US TRIBUTARIES	Number of upstream tributaries	2	3.22	0-19	
Ecobasin	Combination of Omernik (1987) Level III ecoregion and major drainage basin	Savannah Sand Hills			8
		Savannah Atlantic Southern Loam Plains			5
		Savannah Carolina Flatwoods			5
		ACE Sand Hills			12
		ACE Atlantic Southern Loam Plains			24
		ACE Carolina Flatwoods			37
		Lower Santee Sand Hills			5
		Lower Santee Atlantic Southern Loam Plains			12
		Lower Santee Carolina Flatwoods			6
		Pee Dee Sand Hills			18
		Pee Dee Atlantic Southern Loam Plains			34
		Pee Dee Carolina Flatwoods			42

Table 1.2. Group membership and indicator values for four coastal plain fish assemblages.

Scientific Name	Common Name	Group Number	Community Name	Indicator Value	P	Frequency
<i>Notropis cummingsae</i>	Dusky Shiner	1	Fluvial	0.643	0.001	54
<i>Pteronototropis stonei</i>	Lowland Shiner	1	Fluvial	0.588	0.001	45
<i>Etheostoma olmstedii</i>	Tessellated Darter	1	Fluvial	0.488	0.001	64
<i>Percina nigrofasciata</i>	Blackbanded Darter	1	Fluvial	0.436	0.001	33
<i>Noturus leptacanthus</i>	Speckled Madtom	1	Fluvial	0.374	0.001	29
<i>Noturus insignis</i>	Margined Madtom	1	Fluvial	0.363	0.001	32
<i>Etheostoma fricksium</i>	Savannah Darter	1	Fluvial	0.354	0.001	23
<i>Nocomis leptocephalus</i>	Bluehead Chub	1	Fluvial	0.206	0.001	18
<i>Notropis lutipinnis</i>	Yellowfin Shiner	1	Fluvial	0.196	0.002	16
<i>Ameiurus brunneus</i>	Snail Bullhead	1	Fluvial	0.190	0.001	22
<i>Notropis petersoni</i>	Coastal Shiner	1	Fluvial	0.111	0.034	22
<i>Opsopoeodus emiliae</i>	Pugnose Minnow	1	Fluvial	0.077	0.019	5
<i>Umbra pygmaea</i>	Eastern Mudminnow	2	Mudminnow	0.330	0.001	69
<i>Lepomis auritus</i>	Redbreast Sunfish	3	Centrarchid	0.514	0.001	96
<i>Lepomis macrochirus</i>	Bluegill	3	Centrarchid	0.454	0.001	83
<i>Lepomis punctatus</i>	Spotted Sunfish	3	Centrarchid	0.378	0.001	85
<i>Micropterus salmoides</i>	Largemouth Bass	3	Centrarchid	0.303	0.001	66
<i>Anguilla rostrata</i>	American Eel	3	Centrarchid	0.289	0.002	96
<i>Labidesthes sicculus</i>	Brook Silverside	3	Centrarchid	0.127	0.006	12
<i>Lepomis microlophus</i>	Redear Sunfish	3	Centrarchid	0.118	0.028	22
<i>Minytrema melanops</i>	Spotted Sucker	3	Centrarchid	0.113	0.014	17
<i>Perca flavescens</i>	Yellow Perch	3	Centrarchid	0.101	0.005	5
<i>Ameiurus platycephalus</i>	Flat Bullhead	3	Centrarchid	0.086	0.024	9
<i>Notemigonus crysoleucas</i>	Golden Shiner	4	Non-Fluvial	0.631	0.001	73
<i>Centrarchus macropterus</i>	Flier	4	Non-Fluvial	0.520	0.001	67
<i>Enneacanthus gloriosus</i>	Bluespotted Sunfish	4	Non-Fluvial	0.458	0.001	77
<i>Esox americanus</i>	Redfin Pickerel	4	Non-Fluvial	0.433	0.001	175
<i>Aphredoderus sayanus</i>	Pirate Perch	4	Non-Fluvial	0.362	0.001	180
<i>Lepomis gulosus</i>	Warmouth	4	Non-Fluvial	0.355	0.001	105
<i>Lepomis gulosus</i>	Mud Sunfish	4	Non-Fluvial	0.315	0.001	92
<i>Ameiurus natalis</i>	Yellow Bullhead	4	Non-Fluvial	0.298	0.004	99
<i>Erimyzon oblongus</i>	Creek Chubsucker	4	Non-Fluvial	0.290	0.002	85
<i>Lepomis marginatus</i>	Dollar Sunfish	4	Non-Fluvial	0.284	0.002	112
<i>Lepomis gibbosus</i>	Pumpkinseed	4	Non-Fluvial	0.271	0.001	44
<i>Erimyzon sucetta</i>	Lake Chubsucker	4	Non-Fluvial	0.266	0.001	35
<i>Enneacanthus obesus</i>	Banded Sunfish	4	Non-Fluvial	0.225	0.001	17
<i>Elassoma zonatum</i>	Banded Pygmy Sunfish	4	Non-Fluvial	0.202	0.006	55
<i>Amia calva</i>	Bowfin	4	Non-Fluvial	0.186	0.001	21
<i>Etheostoma fusiforme</i>	Swamp Darter	4	Non-Fluvial	0.117	0.046	27

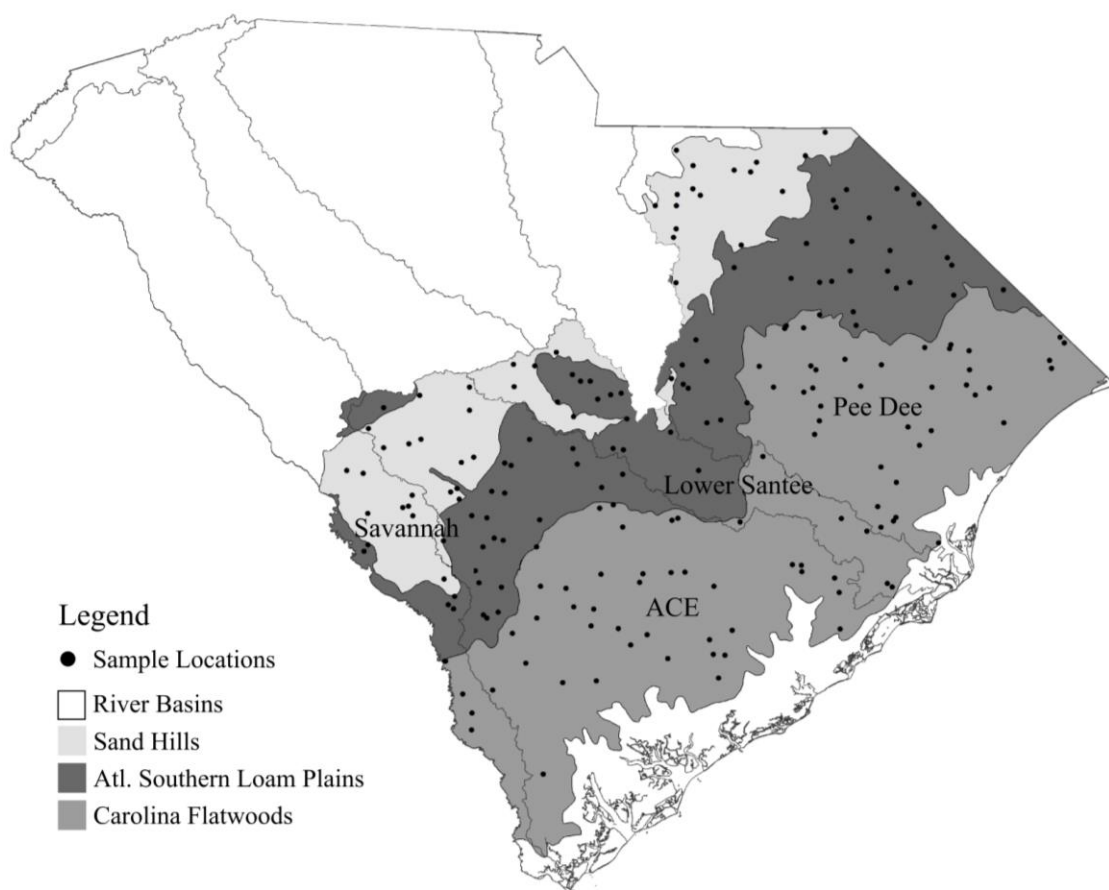


Figure 1.1. Study area showing EPA level IV ecoregions, major drainage basins, and locations of all sampling sites.

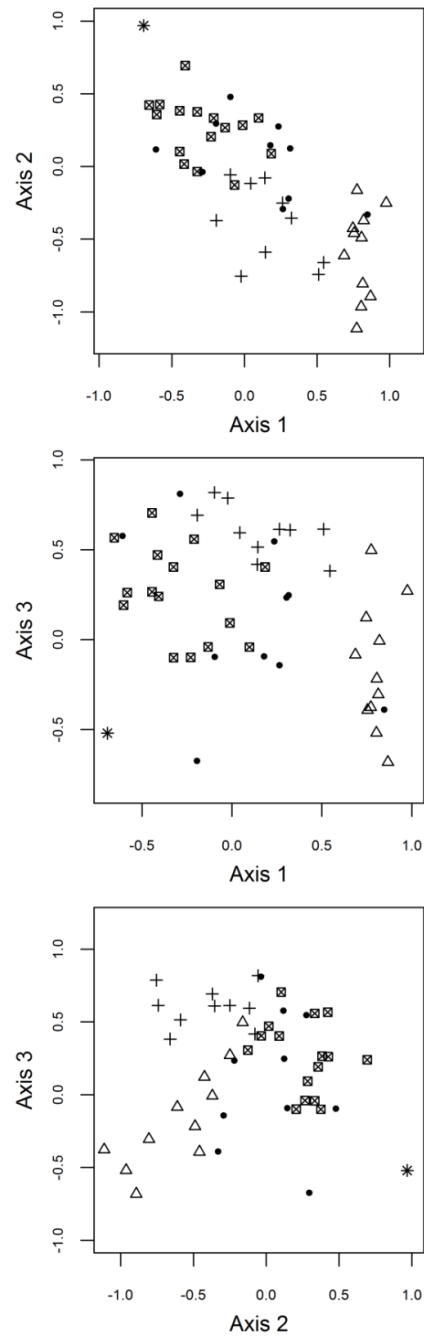


Figure 1.2. Non-metric multidimensional scaling results for first 3 axes. Symbols represent species in sample space, and are individually coded to show their assemblage association as determined by the cluster analysis. Triangles represent members of the fluvial community, stars represent members of the eastern mudminnow community, crosses represent members of the centrarchid community, and squares containing an X represent members of the non-fluvial community.

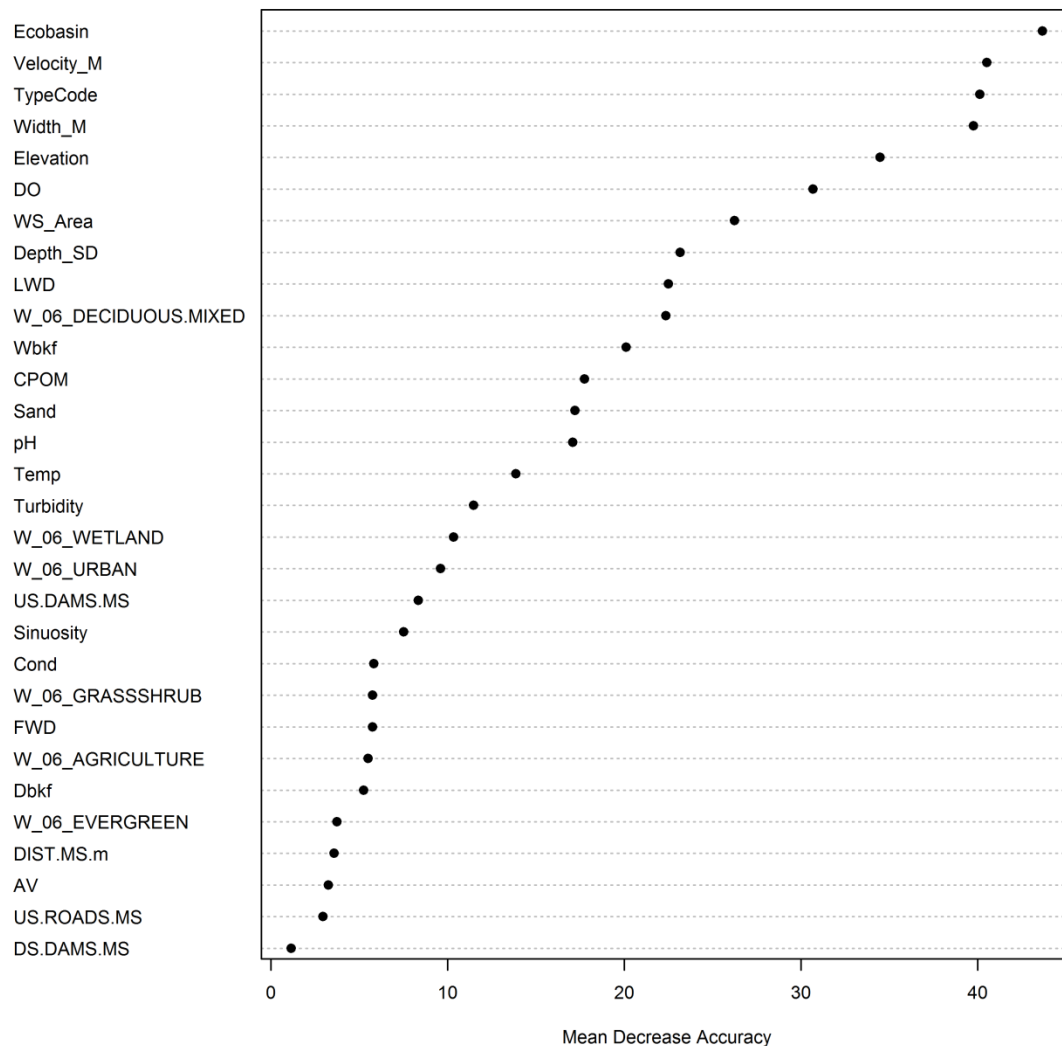


Figure 1.3. Variable importance plot showing top ranked variables from random forests classification for predicting coastal plain taxonomic assemblage membership. Mean decrease in accuracy is the normalized difference of the classification accuracy for the observations excluded from model calibration, and the classification accuracy for the same observations when values of the predictor are randomly permuted. Higher values of the mean decrease in accuracy indicate that a variable is more important to the classification.

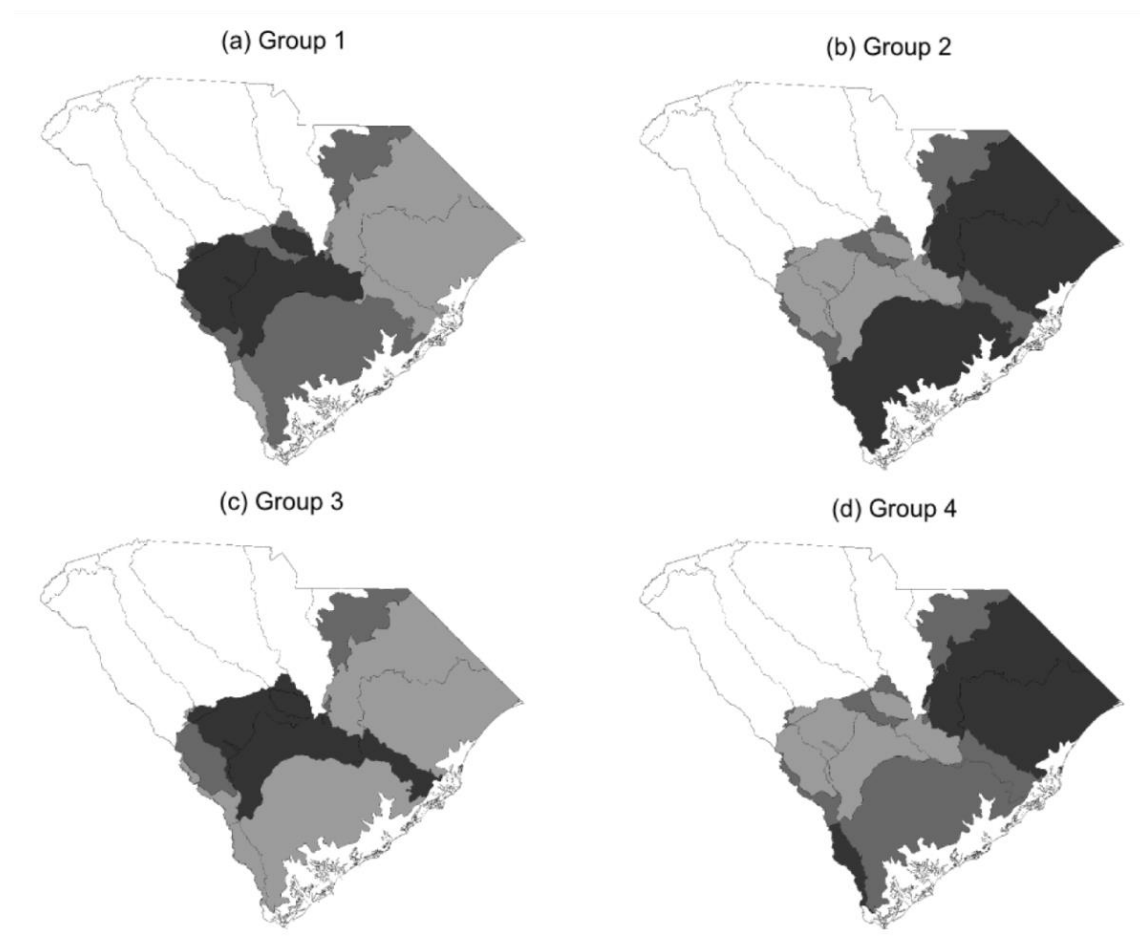


Figure 1.4. Ecobasin was the most important predictor for coastal plain taxonomic group classification. Here, we have shaded ecobasin regions of the coastal plain based on their probability of classification of each of the taxonomic groups (group 1 = fluvial assemblage, group 2 = eastern mudminnow assemblage, group 3 = centrarchid assemblage, group 4 = non-fluvial assemblage). Shaded areas indicate high (dark grey), intermediate (medium grey), and low (light grey) probabilities of classification.

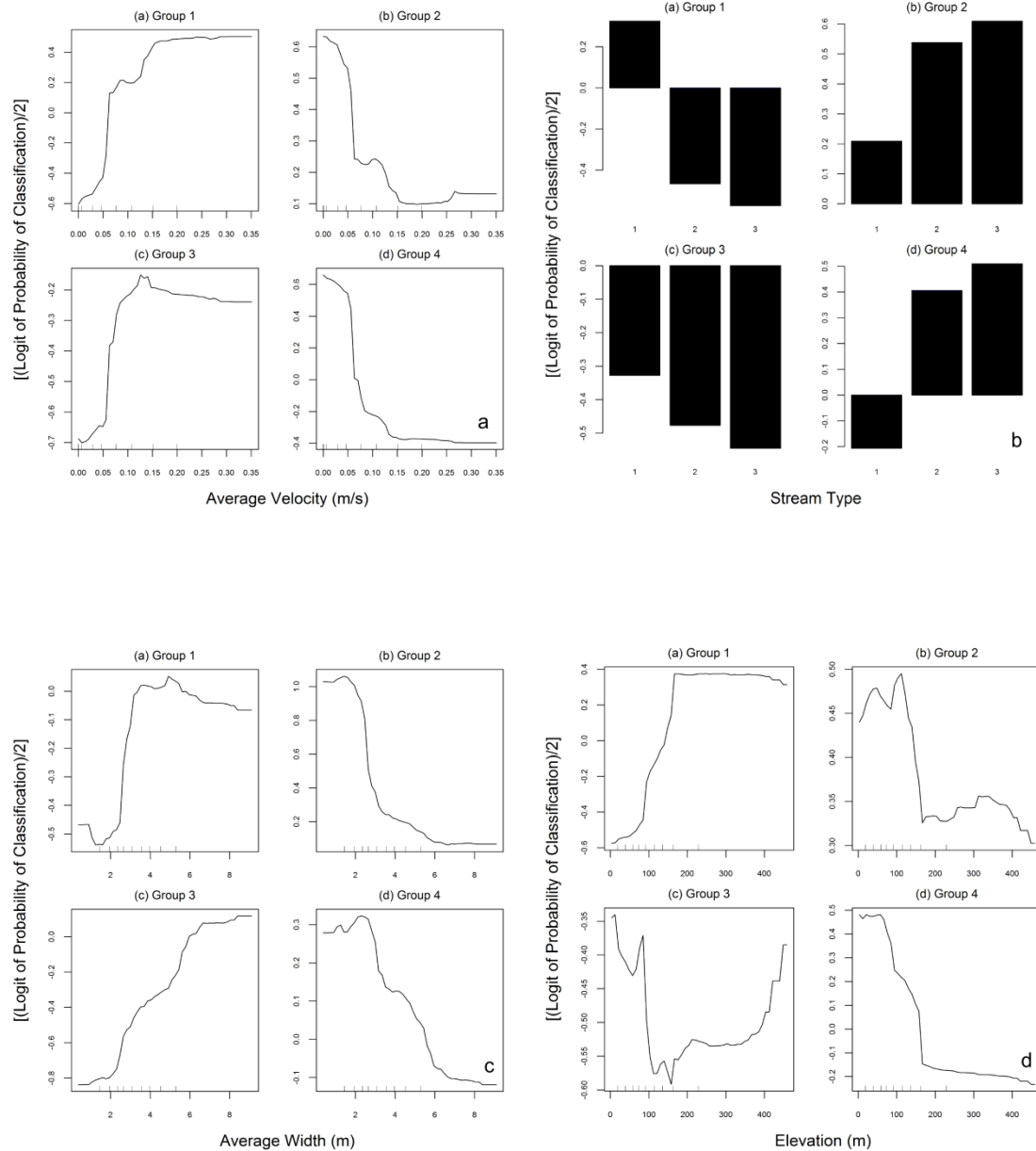


Figure 1.5 a-j. Partial dependence plots for top ranked predictors. Partial dependence plots isolate and examine the behavior of individual predictors on the outcome, while holding the effect of all other predictive variables constant. Partial dependence plots are divided into four quadrants, showing the isolated relationship between each predictor and each individual coastal plain taxonomic assemblage. Group 1 is the fluvial assemblage, group 2 is the eastern mudminnow assemblage, group 3 is the centrarchid assemblage, and group 4 is the non-fluvial assemblage.

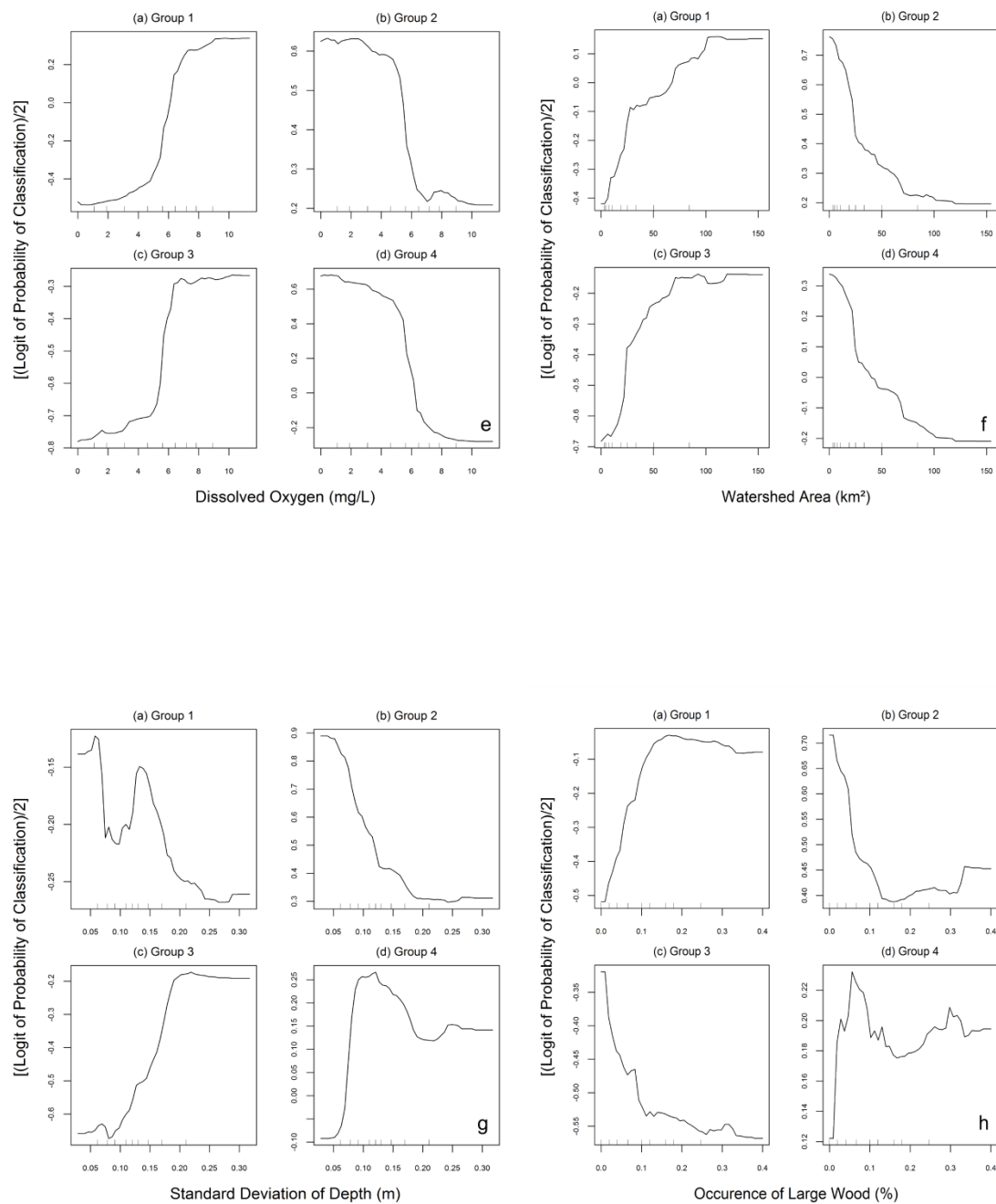


Figure 1.5 a-j continued.

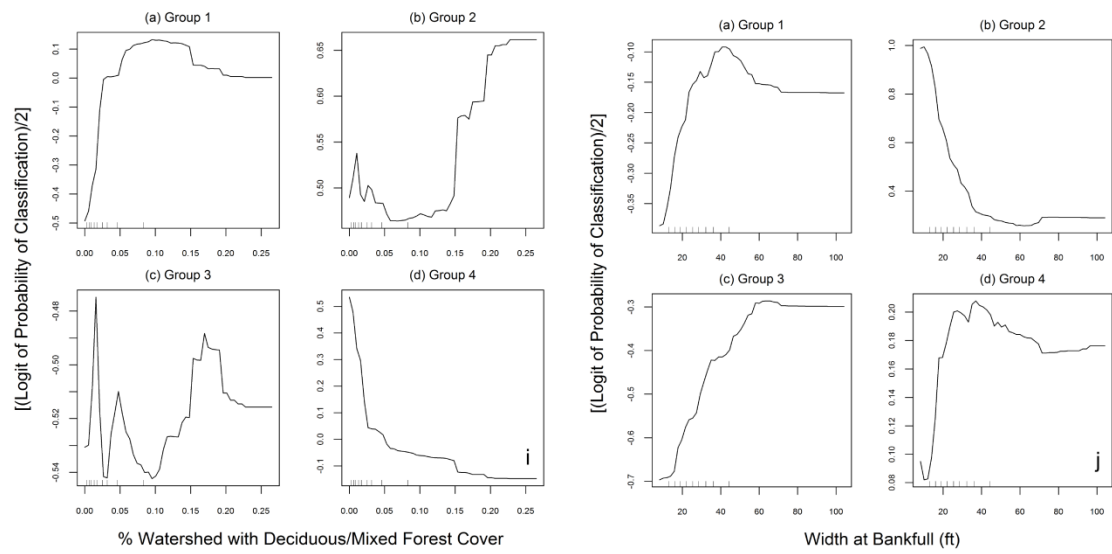


Figure 1.5 a-j continued.

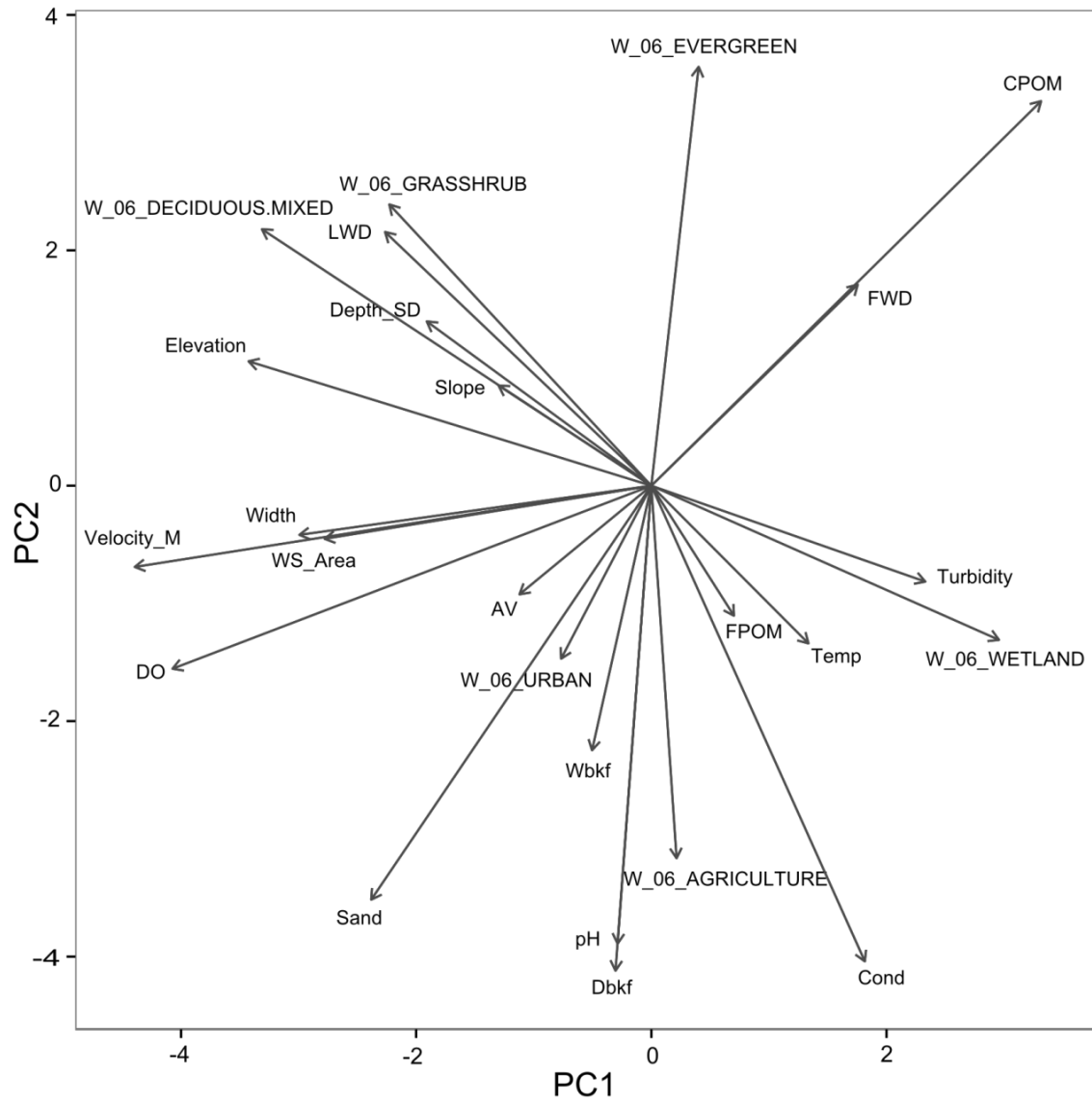


Figure 1.6. Principal components analysis of multi-scale abiotic variables. The length of arrow vectors represents a variables strength of relationship with a given explanatory axis.

CHAPTER TWO

FISH TAXONOMIC AND TRAIT ASSOCIATIONS AMONG MIXED STREAM CHANNEL GEOMORPHOLOGIES IN THE SOUTH ATLANTIC COASTAL PLAIN

Abstract

Hundreds of miles of South Atlantic coastal plain streams have been dramatically altered by channelization over the last 200 years for agricultural, silvicultural, or other anthropogenic endeavors. Although there is some evidence to the contrary, the impacts of channelization on stream habitats and fish assemblages of different regions have generally been negative. Previous research on the impacts of channelization on fishes has largely focused on changes in traditional measures of taxonomic diversity and assemblage-based analyses. Trait-based analyses offer an alternative approach for assessing fish assemblage response to channelization that may enhance our understanding of disturbance/response patterns in South Atlantic coastal plain streams. We sampled habitat and fishes in 163 freshwater coastal plain wadeable streams in South Carolina and categorized streams a priori into 4 channel types based on observations of their gross channel morphology: 1) single channel non-channelized streams, 2) maintained channelized streams, 3) unmaintained (> 5years) channelized streams, and 4) braided swamp-like non-channelized streams. We performed a series of statistical tests to identify significant instream habitat differences among channel types, and evaluated differences in fish assemblages using both taxonomic and trait-based analyses. Our results indicated that channelization significantly influences the instream physicochemical habitat conditions of South Atlantic coastal plain streams, and in turn influences patterns of fish

assemblage structure. Maintained channelized streams retained higher average velocities than unmaintained channelized streams, but both types of channelized streams had fewer structural habitat components, greater indications of water quality degradation, and lacked floodplain connectivity in comparison to unchannelized streams. We found no difference in fish taxonomic diversity metrics among channel types, and taxonomic assemblage-based analyses revealed limited information regarding structural associations. In contrast, our trait-based analysis elucidated species differences among all channelized and non-channelized channel types; principal differences were found in habitat preference, and body size/reproductive ecology. Single channel non-channelized streams were typified by a suite of native rheophilic species, while braided swamp-like streams hosted native rheophobic fishes with high tolerance to low-flow habitats. Although actively maintained channelized streams retained fluvial habitats, they failed to support native rheophilic species. Instead, they were typified by fishes with opportunistic/colonizing life histories common to aquatic systems with low environmental stability and high abiotic stress. Unmaintained channelized streams were typified by predatory species, reflecting the potential for these streams to undergo seasonal dewatering events. Unmaintained channelized assemblages were otherwise similar to those of braided-swamp like streams, indicating the potential for biotic recovery of channelized streams over time. Our study suggests that trait-based analyses may be particularly well suited to elucidating information on ecological response to environmental disturbances in the South Atlantic coastal plain, and their use in

conjunction with taxonomic analyses should provide a fruitful avenue for developing and testing ecological theory of fish assemblage organization in this region.

Introduction

The structure and function of aquatic assemblages are influenced by a myriad of physicochemical parameters as well as the geomorphic context and geological history of the systems they inhabit (Allan 2004; Frissell et al. 1986; Poff 1997). A link between stream geomorphology (*i.e.* channel form) and biota manifests when geomorphological conditions control and define the amount, diversity, and structure of physical habitat conditions available for biological assemblages (Frothingham et al. 2001; Smiley and Dibble 2005; Sullivan et al. 2006). If measures of channel form can be related to instream habitat and fish assemblage characteristics, then channel form classifications may be useful in predicting instream habitat impairment and developing conservation approaches.

The South Atlantic United States coastal plain is a region of low-elevation and low-relief, with a high density of alluvial floodplain stream and wetland networks (Hupp 2000; Sweet and Geratz 2003). Unmodified streams of this region show a high degree of floodplain connectivity, with geomorphic channel forms ranging from single-channel streams to braided and swamp-like channels (Hupp 2000; Hupp et al. 2009; Rosgen 1996, see Chapter 1). However, stream channelization has dramatically altered the natural geomorphic form of large numbers of South Atlantic coastal plain streams over the last 200 years (Hardison et al. 2009; Hupp et al. 2009; Kapsch 2010; Stone et al. 1992). Channelization is the artificial mechanical straightening, deepening, and/or widening of

stream channels (Schneberger and Funk 1971) to control flooding, drain wetlands, provide irrigation, transport goods, and promote soil drainage for agricultural, silvicultural, or other anthropogenic purposes (Brooker 1985; Kapsch 2010; Maxted et al. 2000; Wahl et al. 1997). The impacts of channelization on stream habitats and biological assemblages of different regions have generally been negative (Bayless and Smith 1964; Brooker 1985; Gorney et al. 2012; Oscoz et al. 2005; Schoof 1980; Tarplee et al. 1971), but have also yielded variable and sometimes conflicting results (e.g. Gidley et al. 2012; Kappesser 2002; Stammer et al. 2008). Rationale for such variability includes the influence of study spatial resolution (Smiley and Dibble 2008), sample methods (Frothingham et al. 2001; Takacs et al. 2012), and differences among aquatic habitats (Hardison et al. 2009; Johansson 2013).

Examinations of the impacts of anthropogenic disturbances (e.g. channelization) on biodiversity are deeply rooted in analyses of taxonomic diversity metrics (e.g. richness, evenness, diversity, abundance) and assemblage structure (Doledec et al. 2011; Doledec and Statzner 2010). A known limitation of taxonomic-based analyses is that they vary considerably and perform poorly across biogeographic gradients (Heino 2001; Hewlett 2000; Poff and Allan 1995); this short-coming insinuates a limited ability to distinguish between the effects of an environmental disturbance and a strong natural gradient. Previous investigations of South Atlantic coastal plain fish assemblages indicate that fish assemblages overlap extensively, but are dominantly structured according to natural geomorphic and hydrological gradients that largely obscure potential impacts of landscape and habitat disturbances (see Chapter 1). Such strong natural variation, even

within a single biogeographic region, may limit the efficacy of taxonomic analyses in South Atlantic coastal plain streams (Herlihy et al. 2008).

Trait-based analyses offer an alternative approach for assessing disturbance responses in stream fish assemblages (Doledec and Statzner 2010; Frimpong and Angermeier 2009; Mouillot et al. 2013; Winemiller 2005). Species traits are a collection of life-history and behavioral attributes that influence organismal performances (Frimpong and Angermeier 2010; Violle et al. 2007), and can be expected to reflect the functional relationships between biota and environmental characteristics (Frimpong and Angermeier 2010; Lamouroux et al. 2002; McGill et al. 2006; Poff 1997; Southwood 1977; Townsend and Hildrew 1994). In regions with strong natural gradients that obscure disturbance patterns in fish assemblages, trait-based approaches may provide better information than taxonomic-based approaches regarding species response to disturbance.

In the current study, we examined the impacts of stream channelization on instream habitats and fish assemblages of the South Atlantic coastal plain. Because stream channelization and resultant loss of floodplain connectivity represents profound and fundamental alterations of stream structure and function, we expected that instream habitat and fish assemblages in channelized stream channel types would be dissimilar to those in other unmodified, naturally occurring coastal plain stream channel types. To test this hypothesis we classified test streams to a priori channel type designations based on their gross channel morphologies (2 unmodified channel types, and 2 channelized channel types). We performed a series of statistical tests in order to: 1) identify instream habitat differences among 4 categories of channelized and unchannelized South Atlantic

coastal plain streams, and 2) evaluate differences in fish assemblages using both taxonomic and trait-based analyses. The results of this study should provide insight into the effects of channelization on instream habitats and fish assemblages, and evaluates the utility of taxonomic versus trait-based analyses in discerning the biological impacts of anthropogenic disturbances in South Atlantic coastal plain streams.

Study Site

Data for this study are a subset of a larger evaluation of statewide aquatic resources conducted by the South Carolina Department of Natural Resources (SCDNR) in the spring through fall of 2006-2011, termed the South Carolina Stream Assessment. We sampled 163 wadeable freshwater streams within the EPA level IV Atlantic Southern Loam Plains and Carolina Flatwoods ecoregions, and the Pee Dee, Lower Santee, Ashepoo-Combahee-Edisto (ACE), and Savannah drainage basins of South Carolina's coastal plain, USA (Figure 2.1; Omernik 1987). Sample locations were randomly selected from a probabilistic framework designed by the South Carolina Department of Natural Resources, described in detail elsewhere (Scott 2008; see Chapter 1). Sample locations drained catchments ranging from 0.2 to 154 km² and shared no more than half of their drainage area with any downstream site, limiting the degree of dependence among samples.

Methods

We separated sample sites into 4 'channel type' categories based on our observations of their gross channel morphology. Channel type 1 streams (n = 49) had a single sinuous channel with well-defined banks (non-channelized), and floodplain

connectivity. Channel type 2 streams ($n = 16$) had a single mechanically straightened channel disconnected from the floodplain (channelized), and were actively maintained (regular dredging, mowing of banks, or instream snag removal). Channel type 3 streams ($n = 47$) had a single mechanically straightened channel disconnected from the floodplain (channelized), but were not actively maintained (no signs of maintenance for > 5 years). Channel type 4 streams ($n = 51$) had multiple braided undefined channels or swamp-like characteristics (non-channelized), with full floodplain connectivity.

Habitat Collection

We quantified a range of habitat parameters for each sample reach. Site elevations were obtained in the lab from Terrain Navigator Pro Version 9.2 (Trimble Navigation Limited, Sunnyvale, CA, USA) using the North American Datum 1983 map layer. Slope measurements were taken along stable runs of approximately 90 m in length following techniques described in Harrelson (1994). Stream channel width measurements were taken at the 0, 25, 50, 75, and 100m distances along each sample reach and averaged to obtain mean stream width. Depth, velocity, and substrate measurements were quantified using the ‘zig-zag’ habitat sampling method (Bevenger and King 1995; Scott et al. 2009). This method required traversing a random ‘zig-zag’ longitudinal transect in a downstream to upstream direction along the sample reach, recording depth, velocity, and substrate at 50 randomly selected locations. Inorganic substrate particles were measured in millimeters at the intermediate axis and median particle size was calculated. The vast majority of coastal plain streams contained a median particle size of < 2 mm, therefore we examined inorganic substrates as percent sand (*see* Chapter 1). Organic substrates

were classified into one of the following percent categories: 1) fine particulate organic matter, 2) coarse particulate organic matter, 3) fine woody debris, 4) large woody debris, and 5) aquatic vegetation. If one of the 50 random sampling points fell on a dry section of the stream, that measurement was recorded as ‘dry’ and the total sample was reduced by the number of ‘dry’ points. Physical and chemical data, including water temperature, dissolved oxygen, conductivity, and pH were recorded prior to fish sampling using a YSI 556 MPS[™] multiparameter probe. Turbidity was recorded using a MicroTPW[™] turbidimeter.

Fish Collection

We collected fishes with backpack electrofishers (Appalachian Aquatics Model AA-24) from spring to fall in the years 2006-2011 during base flow conditions. Sample methods followed standard protocols employed by the South Carolina Department of Natural Resources for sampling fish in wadeable streams (Scott et al. 2009). This protocol dictates a three-pass electroshocking method along a stream reach length equivalent to 20x average width (reach length range: 100-200m, median: 100m). We utilized block-nets at both ends of the sample reach unless the reach was sufficiently blocked at one (or both) ends by a natural barrier. All fishes were collected with dip nets (4.8-mm mesh), field identified and enumerated, and released upon sample completion. Specimens that could not be positively identified in the field were preserved in a 90% ethanol solution and returned to the lab for positive identification.

Statistical Analyses

Habitat Differences among Channel Types

We classified streams into 4 channel types based on observed geomorphological differences in channel form. Therefore, we did not perform statistical hypothesis tests of differences in geomorphological measurements, since any null hypotheses regarding no differences in geomorphic measures would be false, a priori (Peterson et al. 2009). We did hypothesize that different channel types created differences in instream habitat characteristics, which in turn influenced the structure of coastal plain fish assemblages. Therefore, we performed one-way analysis of variance (ANOVA) hypothesis testing of differences in habitat characteristics among channel types, and created a classification tree model to identify the habitat parameters that best distinguished among channel types.

We used one-way ANOVAs to test a null hypothesis of no differences in habitat characteristics among the 4 channel types. We $\log_{10}(x)$ -transformed continuous habitat variables and $\arcsine\sqrt{(x)}$ -transformed proportional data. We used the Tukey-Kramer test to make post hoc pairwise multiple comparisons among channel types (Dunnnett 1980). ANOVA and post hoc calculations were performed using the R 2.15.3 statistical software base platform and the DTK package (R Core Development Team 2012).

We next built a classification tree model (Classification and Regression Trees: CART) using untransformed data to identify the most important habitat variables that distinguish among channel types (R package rpart; R Core Development Team 2012). CART models recursively partition observations in a data set into progressively smaller groups that predict the characteristics of the population of sites being studied (Breiman et

al. 1984; De'ath and Fabricius 2000). The CART algorithm can continue to split a dataset until each node contains a single observation of the data set, therefore it is common to set stopping criteria and to 'prune' the model to an optimal tree that contains a sufficient number of splits to describe the data. We set the minimum number of samples to create a split at 10, the minimum number of observations in a terminal node at 7, the complexity parameter at 0.001, and the number of cross-validation procedures at 20. The model was pruned at a size that minimized the cross-validated error.

CART model performance was evaluated with three accuracy measures calculated using the resubstitution method: Proportion Correctly Classified (PCC), Cohen's weighted Kappa statistic (weighted κ), and the area under the receiver operating curve (AUC; Theodoridis and Kourtroubas 2009). Both PCC and weighted κ are derived from the model confusion matrix, which gives the number of actual versus predicted classifications of group membership. PCC performance measures are given in two forms: 1) an overall PCC percentage (accuracy) representing the number of correctly classified cases divided by the total number of cases across all outcome classes, and 2) a measure of accuracy for a specific outcome class (precision). Weighted κ corrects the overall PCC for agreement caused by chance, and gives a value ranging from -1 to 1 (Cohen 1968). A positive value indicates greater agreement between modeled and measured classifications than expected by chance alone, and a negative value indicates less agreement than expected by chance alone. Cohen's weighted κ was calculated using the vcd package in R (R Core Development Team 2012). The AUC is derived from plotting the true positive rate (sensitivity) against the false positive rate (specificity), with each point plotted

representing a sensitivity/specificity pair. The area under the resulting plot is a measure of how well the model correctly classifies groups. AUC values range from 0 to 1, with values > 0.5 indicating better model performance than expected by chance alone (Swets 1988). We used the `ordROC` function in the `nonbinROC` R package in R to calculate AUC values (<http://cran.rproject.org/web/packages/nonbinROC/index.html>).

Taxonomic Diversity and Assemblage Differences among Channel Types

We used one-way ANOVAs to test for differences in fish taxonomic diversity metrics among the four channel types, and used a NPMANOVA with a post-hoc NMDS analysis to test for differences in fish assemblage structure. Taxonomic diversity metrics examined in one-way ANOVAs included richness, evenness, Simpson diversity ($D = 1 - (\sum n(n-1)/N(N-1))$, where n =the total number of fish of a particular species, and N =the total number of fish of all species), and total density (total number of individuals per 100m²). Total density was $\log_{10}(x)$ -transformed. We performed Tukey-Kramer post hoc pairwise multiple comparisons to specify fish metric differences among individual channel types (Dunnett 1980). ANOVAs and post hoc calculations were performed using the R 2.15.3 statistical software base platform and the DTK package (R Core Development Team 2012).

We prepped assemblage data for a NPMANOVA by converting raw fish data to a density matrix (number of individuals by species per 100m²), then performed a $\log_{10}(x+1)$ transformation to reduce the effect of large differences in fish densities among sample sites. Preliminary analysis of the full species matrix revealed an inordinate influence of sites with few species, and several rare species. Therefore, we removed sites from the

analysis if they contained less than 2 species, and we removed species from the analysis if they occurred in less than 3 sites. Rare species generally have little influence on assemblage dynamics and their inclusion in an analysis could significantly distort trends or relationships (Gauch 1982). We additionally removed *Gambusia holbrooki* due to its extreme variability in densities among sites (Lohr and Fausch 1997; Matthews and Marsh-Matthews 2011). The final density matrix contained 148 sites and 55 species.

We tested the multivariate hypothesis of differences in assemblage structure among different channel types using non-parametric multivariate analysis of variance (NPMANOVA; Anderson 2001). After verifying the assumption of homogeneity of group variances, we ran NPMANOVA using the Bray-Curtis distance measure (adonis function in R package ade4; R Core Development Team 2012). Statistical significance was assessed using an F-test derived from 999 random data permutations with $\alpha = 0.05$. There are currently no established post hoc procedures for NPMANOVAs with unbalanced designs, therefore we performed non-metric multidimensional scaling (NMDS) to visualize patterns of differences in fish assemblage structure among channel types (Clarke 1993; Kruskal 1964). NMDS was performed using a random starting configuration, and 1000 runs with real data (R package vegan; R Core Development Team 2012). We used a Monte-Carlo test with twenty iterations and ten randomized runs to determine the probability of obtaining an equal or lower stress value by chance ($\alpha=0.05$). From the NMDS output, we calculated Pearson correlations between individual axes and the fish matrix, and produced plots showing sites coded by their channel type to better interpret and visualize the NPMANOVA outcome.

Trait Differences among Channel Types

We assigned species to a suite of 28 life history traits based on the FishTraits database (Table 2.1; Frimpong and Angermeier 2009). We focused on trait information regarding 1) trophic ecology, 2) body size and reproductive ecology, and 3) habitat/salinity preferences. Several traits in the FishTraits database were categorized at a finer resolution than used for our study, particularly for trophic and reproductive ecology traits, so many traits were excluded or grouped a priori. We used the fourth-corner method to determine functional associations among channel types (fourth corner function in R package ade4; R Core Development Team 2012). The fourth-corner method relates species traits to environmental variables (e.g. channel types) through a fish relative abundance matrix, and analyzes the significance of each bivariate combination of trait and environmental variable separately (Dray and Legendre 2008; Legendre et al. 1997). We followed the two-step permutation testing procedure proposed by Dray and Legendre (2008), with the sequential testing and significance level modifications to control for type I error proposed by ter Braak et al. (2012).

Results

Habitat Differences among Channel Types

We captured considerable variation in habitat conditions across our coastal plain channel types (mean and ranges; Table 2.2). We found significant differences among the four channel types in all habitat variables except average depth, width, and fine particulate organic matter (one-way ANOVA results; Table 2.2). Post hoc tests revealed specific habitat differences among channel types. Elevation and reach slopes were higher

in channel type 1 than in all other channel types. Velocities were higher in channels types 1 and 2 than in channel types 3 and 4. Sand substrates were higher in channel types 1 and 2, and lower in channel types 3 and 4. Aquatic vegetation was higher in channel type 2 than in all other channel types. Course particulate organic matter was lower in channel types 1 and 2, and higher in channel types 3 and 4. Fine wood was lower in type 2 channels than all other channel types. Large wood was higher in channel types 1 and 4 than in channel types 3 and 4. Temperatures were lower in channel types 1 and 2 than in channel types 3 and 4. Dissolved oxygen was higher in channel types 1 and 2 than in channel types 3 and 4. Conductivity was the lowest in channel type 1 (average = 77.83 $\mu\text{S}/\text{cm}$), and highest in channel type 2 (average = 251.50 $\mu\text{S}/\text{cm}$). pH values were greater in channel type 2 than all other channel types. Turbidity was lower in channel type 1 than in either channel type 2 or 3, and also lower in channel type 4 than in channel type 3.

The CART model produced a pruned tree with 4 splits and 5 terminal nodes (Figure 2.2). The model indicated that average velocity was the primary habitat variable that separated channel types 1 and 2 from channel types 3 and 4. Channel types 1 and 2 were further distinguished by the increased prevalence (channel type 1), or scarcity (channel type 2) of large wood. Channel type 4 was typified by slow currents, non-sand substrates, and low conductivity. Channel type 3 was also typified by slow currents, but displayed variability in that some were typified by increased sand substrates, while others were typified by non-sand substrates and high conductivity.

The CART model correctly classified the channel type by habitat differences in 66.21% of our sample sites (PCC), and performed better than chance alone (AUC =

0.83). The weighted kappa statistic indicated a substantial strength of agreement between observed and predicted values (weighted $\kappa = 0.69$). An examination of individual class accuracies (precision) from the output confusion matrix provided additional information on model performance. Channel types 1, 3, and 4 had the highest class precisions at 86.05%, 61.53%, and 70.73% respectively. Channel type 2 had the lowest precision (41.67%), with misclassifications most commonly placed in channel type 3.

Taxonomic Diversity and Assemblage Differences among Channel Types

One-way ANOVAs of fish diversity metrics showed no significant differences among channel types (Table 2.3). However, we did find significant differences in fish assemblage structure among the 4 channel types (NPMANOVA; $F = 6.06$, $P = 0.001$). Our follow-up NMDS resulted in a 3-dimensional solution with a final stress value of 17.23, and a Monte Carlo test indicated significance at $P < 0.001$. We plotted sites in a 3-dimensional ordination space and coded each site according to its channel type, highlighting the nuanced separation of species among channel types (Figure 2.3). Species compositions in channel types 1 and 4 separated most distinctly; species compositions of channel type 3 largely overlapped with those found in channel type 4, and species compositions of channel type 2 showed large variation and overlapped the compositions of both channel types 1 and 4. Species most highly correlated with channel type 1 sites included: *Etheostoma olmstedii*, *Pteronotropis stonei*, *Notropis cummingsae*, *Percina nigrofasciata*, *Noturus leptacanthus*, *Etheostoma fricksium*, *Notropis petersoni* (all $r > |0.3|$). In contrast, species most highly correlated with channel type 4 included: *Umbra pygmaea*, *Esox americanus*, *Aphredoderus sayanus* (all $r > |0.3|$). Species that greatly

overlapped among channel types 3 and 4 included: *Centrarchus macropterus*, *Notemigonus crysoleucas*, *Enneacanthus gloriosus*, *Lepomis gulosus*, *Erymyzon sucetta*, *Lepomis gibbosus*, and *Enneacanthus obesus*. The species assemblages of channel type 2 were highly variable, and showed no clear pattern within the NMDS plots.

Trait Differences among Channel Types

The fourth-corner analysis and associated permutation tests resulted in 27 bivariate relationships among 15 species traits and the 4 channel types that were significantly different from values expected in a randomly organized environment (Table 2.4). Species of single channel non-channelized streams (type 1) were typified by small-bodied, short lived invertivores with preference for lotic habitats and sand/gravel substrates. In contrast, species of braided swamp-like streams (type 4) were typified by fishes that could be long-lived with a large body size, had a late maturation age, and preference for lentic habitats with aquatic vegetation but that lacked sand/gravel substrates. Species traits of maintained channelized streams (type 2) deviated significantly from both of these natural stream conditions, and were typified by low age of maturation, a protracted spawning season, were nest spawners and bearers, and were tolerant to salinity. Species traits of unmaintained channelized streams (type 3) showed a high-degree of overlap with those of braided-swamp like streams (type 4), however were distinguished by more invertivore-piscivores, with smaller potential body size, and were large river associates.

Discussion

The results of this study support our hypothesis that channelization significantly influences the instream physicochemical habitat conditions of South Atlantic coastal plain streams during base flow conditions, and in turn, influences patterns of fish assemblage structure. Our findings are generally consistent with those of other studies that have shown that channelization leads to a cumulative loss of heterogeneous instream habitats (Brooker 1985; Lau et al. 2006; Shields et al. 1994; Wahl et al. 1997). We found that actively maintained streams (type 2) had higher average velocities than non-maintained channelized streams (type 3), but both had fewer structural habitat components (e.g. large wood, fine wood), greater indications of water quality degradation (increased pH, conductivity, turbidity, temperature), and lacked flood plain connectivity in comparison to the natural non-channelized streams of the region (types 1,4).

Fish taxonomic diversity and assemblage-based analyses revealed limited information regarding structural associations among channel types, and displayed difficulty in discerning fish assemblage response to channelization against the backdrop of a strong natural hydrological gradient that strongly influences patterns in coastal plain fish distribution (Poff and Allan 1995; see Chapter 1). In contrast, our trait-based analysis elucidated species differences among all channelized (types 2,3) and non-channelized (types 1,4) channel types, providing support for the theoretical expectation that species traits that promote local persistence should change along an environmental disturbance gradient (Frimpong and Angermeier 2010; McGill et al. 2006; Townsend and Hildrew 1994).

Habitat Differences among Channel Types

Both single channel non-channelized streams (type 1) and braided swamp-like streams (type 4) occur naturally throughout the South Atlantic coastal plain, and channelization dramatically alters the natural stream habitats that these channel types provide. We distinguished between maintained and unmaintained channelized streams (types 2, 3) a priori, and our ANOVA and CART analyses revealed a number of habitat differences between these two channel types (i.e. average velocity, sand, CPOM, AV, temperature, dissolved oxygen). However, several habitat similarities shared by these two channelized channel types highlighted the overarching negative impacts of channelization (i.e. lack of floodplain connectivity, degraded water quality, reduced structural habitat), and were consistent with the findings of previous research (Brooker 1985; Evans et al. 2007; Lau et al. 2006; Shields et al. 1994; Wahl et al. 1997).

Floodplain connectivity and water quality are tightly linked in the South Atlantic coastal plain, where active floodplains trap large amounts of sediments, associated nutrients, and contaminants (Hupp 2000; Mitsch and Gosselink 2000; Rheinhardt et al. 1998). Channelization disrupts this important ecosystem function, and leads to degraded water quality conditions that can have damaging chronic effects on biota over time (Cooper 1993). The loss of structural habitat (e.g. large wood, fine wood) is also a disproportionately large problem for coastal plain streams, where few other stable substrates are available for fishes (Benke et al. 1985). Increased physical habitat complexity is known to support more biologically diverse and stable fish assemblages (Gorman and Karr 1978), by increasing available habitat, providing food resources,

spawning substrate, and protective cover (Angermeier and Karr 1984; Crook and Robertson 1999; Monzyk et al. 1997).

Actively maintained (type 2) and unmaintained (type 3) channelized stream habitats were primarily distinguished by differences in their average velocities. Actively maintained channelized streams are commonly dredged at a slope, and had high average velocities that were similar to single channel non-channelized streams. Stream flow is a key habitat constituent for South Atlantic coastal plain fishes (see Chapter 1), as it has a major influence on patterns of fish habitat use related to habitat volume, substrate and cover composition, temperature, and dissolved oxygen (Olden and Kennard 2010; Poff and Allan 1995; Poff et al. 1997; Roy et al. 2005). Certain native coastal plain fish species are flow-dependent for part or all of their life cycle (Rohde et al. 2009), and it is possible that actively maintained channelized streams provide suitable hydrological habitats for these species. However, other negative physicochemical attributes (e.g. degraded water quality, reduced structural habitat) may preclude these sensitive fluvial taxa, despite the presence of flow.

Un-maintained channelized streams had slow average velocities, similar to braided swamp-like streams. Unmaintained channelized streams retain excess sediments and fine/course organics that accumulate over time, which leads to decreased flows and a homogenous, organic-laden benthos (Hupp et al. 2009; Simon and Hupp 1992). Although these streams are not-maintained and therefore in a process of geomorphic recovery, they are unlikely to lose their archetypal straightened channels over time, but may become slightly wider and shallower until their banks stabilize (Hupp et al. 2009). Regardless,

numerous native coastal plain fishes are tolerant of low-flows and resultant low dissolved oxygen conditions that occur naturally throughout the region, therefore the low-flows present in unmaintained channelized streams do not necessarily preclude a native suite of coastal plain fishes. However it is possible that the general lack of habitat structural components and degraded water quality of unmaintained channelized streams may affect fish structure.

Taxonomic Diversity and Assemblage Differences among Channel Types

The majority of published research regarding the impacts of channelization has examined differences in taxonomic diversity metrics. Although there is some evidence to the contrary (Gidley et al. 2012; Kappesser 2002; Stammel et al. 2008), the prevailing ecological consensus is that channelization decreases instream habitat complexity, which in turn causes declines in richness, evenness, diversity, density, biomass, biotic integrity scores, and total numbers (Brooker 1985; Frothingham et al. 2001; Gorney et al. 2012; Huggins and Moss 1974; Oscoz et al. 2005; Pilcher et al. 2004; Shields et al. 1994). We found that taxonomic diversity metrics (richness, evenness, Shannon diversity, total density) did not significantly differ among channel types, despite identified habitat differences. In the absence of additional information, we might conclude that channelization has no impact on South Atlantic coastal plain fish assemblages. However, similar metric values across channel types indicated species turnovers and overlap rather than net losses or gains. The South Atlantic coastal plain displays a strong natural hydrological gradient, with healthy streams ranging from perennial flowing streams (e.g. type 1), to low-flow or even stagnant streams (e.g. type 4). The hydrologies of maintained

and unmaintained channelized streams are both captured within this naturally variable hydrological regime. A unique suite of native coastal plain fishes shows a large range of tolerances and adaptations to these disparate hydrological conditions (see NMDS results; also Chapter 1; Rohde et al. 2009). As given hydrological conditions change, intolerant species are replaced by species better suited to current conditions. Such variation along a strong natural hydrological gradient largely obscures our ability to discern the impacts of an environmental disturbance (see Chapter 1). As such, taxonomic diversity metrics are unlikely to be good indicators of disturbance in the South Atlantic coastal plain.

Our assemblage-based taxonomic analysis (NPMANOVA) indicated significant fish assemblage differences among channel types, yet the follow-up NMDS yielded limited information regarding specific assemblage associations with stream types, and inferred a high degree of species overlap among channel types. The NMDS did show a strong assemblage separation between single channel non-channelized streams and braided swamp-like streams, which highlighted an overall assemblage response to natural hydrological differences between the two channel types (Poff and Allan 1995), and provided support for our assertion regarding species turnover or overlap among channel types. Species associated with single channel non-channelized streams included shiners, darters, and madtoms with life-history requirements for sustained flow. In contrast, species associated with braided swamp-like streams tended to be wetland specialists, with specific tolerances and specialized adaptations for low-flow conditions. Fish assemblages of non-maintained channelized streams tended to overlap extensively with those of braided swamp-like streams, and included several common coastal plain centrarchids and

tolerant cyprinids/catostomids. Our assemblage analysis (NMDS) did not reveal clear assemblage association with maintained channelized streams.

Our habitat analysis revealed that channelized streams (types 2,3) displayed instream habitat conditions unlike their natural counterparts (types 1,4), and therefore represented an environmental disturbance. Proper biological indicators should be sensitive to, and show predictable variation across ecological disturbance gradients (Dale and Beyeler 2001). Taxonomic diversity and assemblage-based analyses revealed a general turnover in fluvial to non-fluvial species along a natural geomorphic-hydrological gradient, but largely failed to discern specific biotic impacts of channelization. Taxonomic diversity metrics and abundance distributions summarize the numerical structure and abundance variability of a population, but do not fully consider biological identity and functional differences among species, which may be more important in their explanation of assemblage response to ecosystem processes and environmental disturbances (Villegger et al. 2010). We conclude that taxonomic diversity metrics and abundance analyses, if used alone, may be inadequate to in assessments of environmental disturbances in South Atlantic freshwater stream systems.

Trait Differences among Channel Types

Our trait-based analysis better elucidated species differences among channel types than taxonomic diversity metrics and assemblage-based analyses, showing strong potential as a tool to evaluate the impacts of environmental disturbances on South Atlantic coastal plain fish assemblages. The principal functional associations among channel types were largely driven by differences in habitat preference (e.g. flow,

substrate) and body size/reproductive ecology (maxtl, matuage, longevity), while trophic ecology played a lesser role. The fourth-corner analysis reiterated the importance of flow dynamics in predicting patterns of coastal fish distributions among channel types; the association between hydrology and fish life history strategies is supported by a strong body of research (Olden et al. 2006; Tedesco et al. 2008; Vila-Gispert et al. 2005; Winemiller 2005; Winemiller and Rose 1992). The fluvial habitats of single channel non-channelized streams host a unique suite of native rheophilic fishes (cyprinids, percids, and ictalurids). Lotic coastal plain habitats are primary zones of invertebrate production, the major food source for benthic percids and drift-feeding cyprinids, who typically exhibit optimal feeding behaviors at certain velocity ranges (Grossman et al. 2002; Hill and Grossman 1993). While our analysis did not discern reproductive trait associations, many of these rheophilic species are also lithophilic spawners who require clean inorganic substrates (e.g. sand, gravel) in flowing oxygenated waters to reduce egg mortality. In sharp contrast, the lentic habitats of braided swamp-like streams were largely inhabited by rheophobic fishes that exhibit high tolerance to low-flow or fluctuating water levels. Some have specific adaptations to low-flow conditions including the capability of gulping atmospheric air using a phytostomous swim bladder, and the ability to aestivate in moist soils (Rohde et al. 2009). Others are highly tolerant to low pH, low dissolved oxygen, and high temperatures. Large-bodied, late maturing swamp-associated species (e.g. *Amia calva*, *Lepisosteus osseus*) commonly use braided swamp-like stream habitats as spawning and juvenile rearing grounds (Rohde et al. 2009).

The impact of channelization on trait structures was more evident in actively maintained channelized streams than non-maintained channelized streams. Actively maintained channelized streams were typified by fishes with colonizing or opportunistic life history attributes including protracted breeding seasons and low age of sexual maturation. Opportunistic and/or colonizing life history strategies are common in aquatic systems with low environmental stability and high abiotic stress (Poff and Ward 1990; Winemiller 1992; Winemiller 2005). Several studies in other regions have found an increase in small-bodied opportunistic species associated with channelization, indicating this response may be general (Frothingham et al. 2001; Lau et al. 2006; Oscoz et al. 2005; Pilcher et al. 2004; Shields et al. 1994). Although actively maintained channelized streams retained a fluvial habitat, their fish assemblages were not typified by traits of coastal plain fluvial specialists, indicating that some aspect of habitat disturbance associated with active channelization (e.g. structural degradation, water quality degradation, hydrological variability) limited the ability for those species to thrive.

Non-maintained channelized streams were similar in trait composition to braided swamp-like streams, with fishes showing affinities for and/or tolerances to low-flow habitats. Non-maintained channelized stream species traits were distinguished from those of braided swamp-like systems in that they were typified by smaller-bodied large river invertivore-piscivore predator species, such as centrarchids (e.g. *Enneacanthus*, *Lepomis*). Although we failed to document information regarding seasonal or long-term hydrologic regime differences among channel types, our field observations indicated that non-maintained channelized streams were particularly susceptible to periods of seasonal

dewatering or near-dewatering. Several studies have suggested that the distribution of fishes are shaped, in part, by the interactions between life history strategies and patterns of predictability and variability in hydrologic regimes (Fausch et al. 2002). Seasonal dewatering may increase the proportion of predators (e.g. centrarchids) while decreasing the proportion of invertivores, as increased competition among species is instigated by dwindling food and habitat resources (DeAngelis et al. 1997).

Taken as a whole, our results supported our hypothesis that the instream habitats and fish assemblages of channelized streams are dissimilar to those of unmodified, naturally occurring stream channel types of the South Atlantic coastal plain. Actively maintained channelized streams retained fluvial habitats, but failed to support native fluvial specialist assemblages, rather they hosted a suite of opportunistic and/or colonist species. Unmaintained channelized streams showed an association with predatory species whose abundances may reflect the potential for these streams to undergo seasonal variability in hydrological conditions and stream drying. Unmaintained channelized stream assemblages were otherwise similar to those of braided swamp-like streams, indicating potential for the biotic recovery of channelized streams over time.

Our results indicated that fluvial specialists tend to predominantly inhabit single-channel non-channelized streams, and have limited tolerance to actively maintained or unmaintained channelized streams, as well as non-channelized braided swamp-like streams. Therefore, the loss of fluvial habitats found in single channel non-channelized South Atlantic coastal plain streams to channelization or other anthropogenic disturbances may lead to the extirpation of the fluvial specialists dependent on these

habitats. Management efforts should focus on the preservation of these fluvial habitats where they exist.

We suggest that trait-based analyses may be particularly well-suited to elucidating information on ecological response to environmental disturbances in the context of a strong natural gradient (e.g. flow, salinity, elevation), and their use in conjunction with taxonomic analyses may provide a fruitful avenue for developing and testing ecological theory of fish assemblage organization across the South Atlantic coastal plain. Our work builds on evidence that geomorphic characteristics are important local-scale determinants of coastal plain stream habitats and fish assemblages, and further enhances our understanding of the hierarchy of factors that influence South Atlantic coastal plain fish diversity and organization.

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Table 2.1. Traits derived from FishTraits database used in data analysis.

Trait Code	Data Scale	Description
<i>Trophic Ecology</i>		
benthic	Binary	Benthic feeder
surwcol	Binary	Surface or water column feeder
invertivore	Binary	Invertebrates and larval fish
invertivore-piscivore	Binary	Invertebrates/larval fish and larger fish, crayfish
omnivore	Binary	Feeds on herbivore, invertivore, and invertivore-piscivore
<i>Body Size / Reproductive Ecology</i>		
maxtl	Continuous	Maximum total length (cm)
matuage	Continuous	Mean, median, or modal age at maturity for females (years)
longevity	Continuous	Longevity based on life in wild (years)
fecundity	Continuous	Maximum reported fecundity
serial	Binary	Serial or batch spawner
matlength	Continuous	Mean total length at maturity for females (cm)
eggsize	Continuous	Mean diameter of mature (fully yolked) oocytes (mm)
season	Continuous	Length of spawning season (months)
A1	Binary	Nonguarders, open substrate spawners
A2	Binary	Nonguarders, brood hiders
B1	Binary	Guarders, substratum choosers
B2	Binary	Guarders, nest spawners
C	Binary	Bearers (internal and external), substrate indifferent
<i>Habitat / Salinity Preferences</i>		
muck	Binary	Muck substrate
sand	Binary	Sand substrate
gravel	Binary	Gravel substrate
vegetat	Binary	Aquatic vegetation
debrdetr	Binary	Organic debris or detrital substrate
lwd	Binary	Large wood substrate
largeriv	Binary	Medium to large river
creek	Binary	Creek
lotic	Binary	Moderate and/or fast current
euryhaline	Binary	Salinity tolerance

Table 2.2. Habitat ranges, overall means, and means (\pm SD) by channel type. *P*-values are associated with results of one-way ANOVAs with channel type (1,2,3,4) as the independent variable. Bolded italics indicate statistical significance.

Habitat Variable	Unit	Range	Mean	Channel Type 1	Channel Type 2	Channel Type 3	Channel Type 4	<i>P</i>
<i>Physical Parameters</i>								
Elevation	m	0.92-83.32	28.20	44.77 (21.69)	16.87(13.89)	22.32(12.39)	19.96(16.61)	<i>0.000</i>
Slope	%	0-.007	0.001	0.0017(0.0015)	0.0007(0.0008)	0.0009(0.001)	0.001(0.001)	<i>0.017</i>
Average Width	m	1-8.69	3.31	3.72(1.52)	3.34(1.06)	2.99(1.48)	3.18(1.42)	0.094
Average Velocity	m/s	0-0.35		0.13(0.07)	0.105(0.108)	0.03(0.04)	0.02(0.02)	<i>0.000</i>
Average Depth	m	0.07-0.58	0.25	0.27(0.10)	0.24(0.17)	0.27(0.14)	0.23(0.09)	0.312
Standard Deviation of Depth	m	0.03-0.28	0.13	0.14(0.05)	0.09(0.04)	0.12(0.05)	0.13(0.05)	<i>0.002</i>
<i>Substrate Parameters</i>								
Sand	%	0-0.80	0.27	0.37(0.14)	0.45(0.26)	0.23(0.19)	0.14(0.17)	<i>0.000</i>
Aquatic Vegetation	%	0-0.96	0.08	0.05(0.05)	0.23(0.19)	0.08(0.17)	0.05(0.11)	<i>0.000</i>
Fine Particulate Organic Matter	%	0-0.47	0.06	0.07(0.09)	0.04(0.05)	0.06(0.08)	0.06(0.08)	0.663
Course Particulate Organic Matter	%	0-0.88	0.30	0.17(0.10)	0.14(0.20)	0.34(0.23)	0.44(0.21)	<i>0.000</i>
Fine Wood	%	0-0.49	0.12	0.11(0.06)	0.04(0.05)	0.13(0.10)	0.15(0.08)	<i>0.000</i>
Large Wood	%	0-0.40	0.12	0.16(0.09)	0.03(0.03)	0.08(0.09)	0.13(0.10)	<i>0.000</i>
<i>Chemical Parameters</i>								
Temperature	°C	13.15-28.86	22.13	20.91(3.90)	22.7(3.81)	22.69(3.11)	22.72(2.93)	<i>0.028</i>
Dissolved Oxygen	mg/L	0.2-11.37	4.96	7.06(2.11)	6.47(2.54)	4.22(2.58)	3.03(2.23)	<i>0.000</i>
Conductivity	µS/cm	14-708	118.15	77.83(49.53)	251.5(198.21)	118.78(53.47)	118.19(71.39)	<i>0.000</i>
pH		4.92-8.06	6.73	6.73(0.58)	7.21(0.84)	6.71(0.60)	6.61(0.54)	<i>0.039</i>
Turbidity	NTU	1.03-59.29	10.22	6.05(4.16)	13.19(10.20)	15.02(17.76)	9.29(9.19)	<i>0.001</i>

Table 2.3. Fish diversity metric ranges, overall means, and means (\pm SD) by channel type. *P*-values are associated with results of one-way ANOVAs with channel type (1,2,3,4) as the independent variable. Bolded italics indicate statistical significance.

Fish Diversity Metric	Range	Mean	Channel Type 1	Channel Type 2	Channel Type 3	Channel Type 4	<i>P</i>
Richness	3-25	12	14(6)	12(5)	12(5)	12(5)	0.06
Evenness	0.38-0.98	0.75	0.73(0.12)	0.81(0.11)	0.78(0.11)	0.74(0.13)	0.11
Simpson Diversity	0.32-0.91	0.75	0.75(0.14)	0.73(0.14)	0.76(0.12)	0.74(0.15)	0.77
Total Density	3.8-372.2	51.9	55.39(41.5)	52.34(36.69)	38.67(23.3)	60.13(72.7)	0.41

Table 2.4. Significant species and trait relationships among channel types based on 4th corner analysis. Abbreviations and codes are found in Table 2.1. Positive and negative signs indicate directionality of bivariate relationship between trait and channel type. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < .001$

Trait Code	Channel Type 1	Channel Type 2	Channel Type 3	Channel Type 4
<i>Trophic</i>				
invertivore	+ *			- *
invertivore-piscivore			+ *	
<i>Body Size / Reproductive Ecology</i>				
maxtl	- *			+ *
matuage		- *	+ *	+ *
longevity	- *		+ *	+ *
season		+ **		
A2		- *		
B1		+ *		
C		+ **		
<i>Habitat</i>				
sand	+ *			- *
gravel	+ *			- **
vegetat	- **		+ *	+ **
largeriv			+ *	
lotic	+ ***		- ***	- **
euryhaline		+ **		

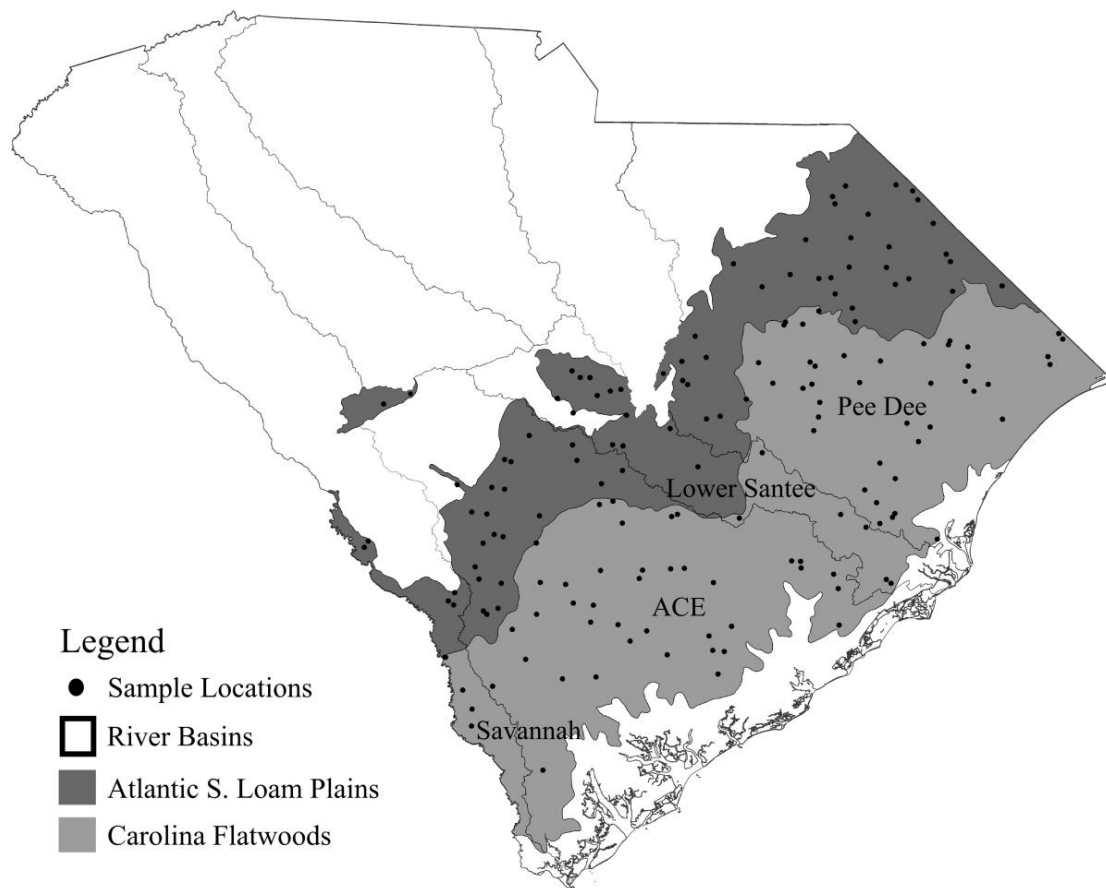


Figure 2.1. Study area showing EPA level IV ecoregions, major drainage basins, and locations of all sampling sites.

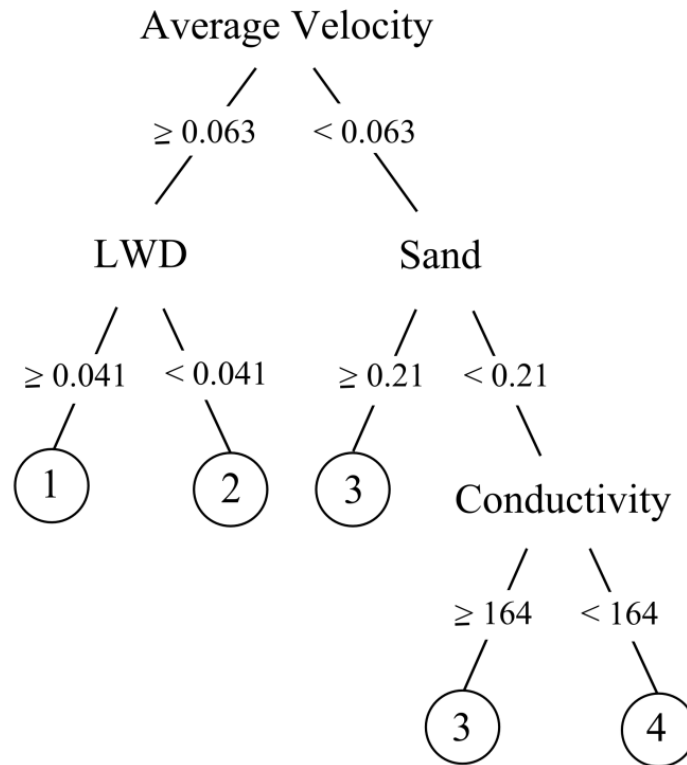


Figure 2.2. Classification tree from the Classification and Regression Tree (CART) model. Values below explanatory variables indicate splitting criteria (e.g. if a site had ≥ 0.063 m/s average velocity, then it was placed into the group to the left of the branch, otherwise it was placed on the branch to the right). Numbers in circles indicate channel type (1,2,3,4) terminal nodes.

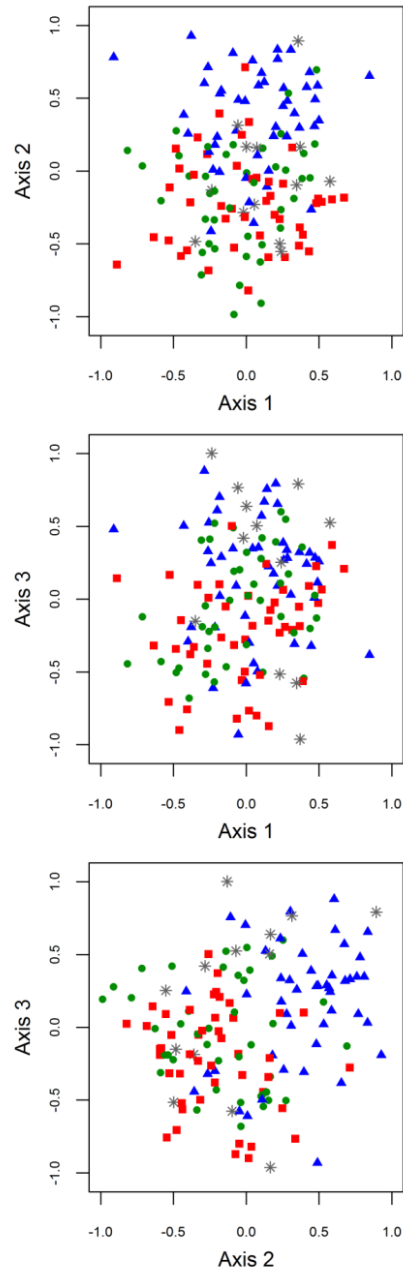


Figure 2.3. Non-Metric Multidimensional Scaling (NMDS) follow-up to NPMANOVA analysis. Symbols represent sites, and are coded according to channel type. Blue triangles represent channel type 1, gray stars represent channel type 2, green circles represent channel type 3, and red squares represent channel type 4.

CHAPTER THREE

THE EFFECTS OF MULTIPLE DAM REMOVALS ON THE FISH ASSEMBLAGE
OF TWELVEMILE CREEK, PICKENS COUNTY, SOUTH CAROLINA

Abstract

Dam removal is considered an effective tool for restoring ecological integrity to rivers and streams, yet few studies have investigated the impacts and recovery of fish assemblages after dam removal(s), and virtually no published research has emerged from dam removals in the southeastern U.S. This study examines the effects of multiple dam removals on the instream habitat and fish assemblages of Twelvemile Creek, a tributary to the Lake Hartwell Reservoir, located in Pickens County, South Carolina. We collected habitat and fish data above and below two removed dams, and from upstream and downstream reference sites, for an approximate timeframe of 5-years prior and 2.5-years after dam removals. We evaluated ecological impacts and recovery by examining changes in habitat (depth, flow, substrate), fish metrics (total density, taxa richness, benthic invertivore density, insectivorous cyprinid density, round-bodied sucker density, native centrarchid density, non-native species density), and fish assemblage structure over time. The bulk of instream habitat changes occurred within 1-year of each dam removal; major geomorphic adjustments led to dramatically increased flow rates and shifts from fine to coarse/bedrock substrates in both former impoundments. However, we found no significant habitat changes in downstream free-flowing sites, despite field observations that indicated persisting deposited sediment for the duration of the study, with greater deposition in the vicinity of the downstream-most removed dam. Previously

lentic-dominated fish assemblages at former impounded sites generally shifted to a lotic-dominated structure within 6-months (upper-removed dam), and 1-1.5 years (lower-removed dam) after dam removal. Despite these prominent assemblage shifts, we found impacts on benthic invertivore density at sites flanking the upper-removed dam at 2.5-years post dam removal, and impacts on total density, richness, benthic invertivore density, and native centrarchid density at sites flanking the lower-removed dam at 2-years post dam removal. These findings suggested that multiple dam removals had a cumulative downstream increase in negative impacts on fish assemblages. We also observed a sharp increase in non-native density following the removal of the lower-most dam, led by captures of *Micropterus henshalli*, a non-native species introduced to the downstream Lake Hartwell reservoir in the 1980s that is known to reduce native *Micropterus coosae* populations through introgressive hybridization. We routinely captured *Micropterus coosae* at all sample sites both before and after dam removals, whereas we only captured *Micropterus henshalli* in post dam removal samples. As such, our study elucidated the potential for tributary dams to act as barriers that protect native lotic species from the influence of reservoir taxa; such phenomena may be exacerbated in southeastern U.S., where impoundment and reservoir density is extremely high. Although dam removal can have ecological trade-offs and short-term disturbance impacts, we demonstrated that dam removal can reverse many of the negative impacts dams have on fish assemblages, primarily through the restoration of high-quality lotic habitats required by native riverine species. Our findings suggest that fish assemblages in high-gradient

southeastern U.S. systems are likely to recover once habitat disturbances and sediment loads are fully reduced, assuming highly vulnerable or sensitive species are not at risk.

Introduction

United States waterways are among the most dammed in the world, boasting over 87,300 recorded dams, and numerous others too small for national registration (Smith *et al.*, 2002; USACE, 2013). The dam building binge of the mid-nineteenth to mid-twentieth centuries has quickly become a major socio-political and economic issue of today, as the environmental costs of dams have been realized, and financial costs for maintenance and repair of ageing dams have steadily risen (ASCE 1997; Bednarek, 2001; Born *et al.*, 1998; Stanley & Doyle, 2003; Walter & Merritts, 2008). Resultantly, dam removal has increasingly been used as a restoration tool intended to mitigate future economic and societal costs, as well as reestablish natural ecological, hydrological, and biological conditions of riverine systems (American Rivers, 2002). Over 1000 dams have been removed from U.S. streams and rivers to date (American Rivers, 2014). However, there remains a limited number of published studies examining the ecological impacts of dam removal, and virtually no research has emerged from the southeastern U.S., despite the fact that the density of both existing and removed dams is relatively high in this region (Graf, 1999; Helms *et al.*, 2011; American Rivers, 2014)

The construction of dams and impoundments was extensive in southeastern U.S. rivers and streams over the last 100-200 years, primarily for hydroelectricity, recreation, water-storage, and irrigation (Graf, 1999; Jenkins, 1970). Large hydroelectric dams have dramatically altered the native hydrological conditions of almost all large rivers of this

region, and small and low-head dams are even more numerous and widespread in small rivers and streams (Graf, 1999; USACE, 2013). Dams degrade lotic habitats by altering the natural hydraulic regime, thermal regime, nutrient processing, physical habitat, benthic substrate composition, and longitudinal connectivity of aquatic ecosystems (Bednarek, 2001; Ligon, Dietrich & Trush, 1995; Petts, 1984). Consequently, dams alter the composition, abundance structure (Martinez *et al.*, 1994; Santucci, Gephard & Pescitelli, 2005; Taylor, Knouft & Hiland, 2001), and longitudinal distribution of native fish assemblages (Winston, Taylor & Pigg, 1991; Wunderlich, Winter & Meyer, 1994).

Removing dams causes a short-term ecological disturbance that disrupts and reconfigures the existing physical environment. Dam removal cannot be assumed to return an aquatic ecosystem to pre-dam conditions, rather is likely to create a novel system that resides somewhere on a continuum of partial recovery to pre-dam conditions (Doyle *et al.*, 2005; Dufour & Piegay, 2009). The timing and extent of the recovery process is largely dictated by the characteristics of dam removal, the geomorphic conditions of the watershed, and the life history characteristics of biotic populations of interest (Doyle *et al.*, 2005). The removal of small dams can be expected to restore lotic habitats within former impounded reaches (Bushaw-Newton *et al.*, 2002; Stanley & Doyle, 2002), and can have long-term biological benefits such as the replacement of tolerant habitat generalist taxa with sensitive habitat specialist taxa (Catalano, Bozek & Pellett, 2007; Kanehl & Lyons, 1997), and improved fish migration (Catalano, Bozek & Pellett, 2007; Schmetterling, 2003). However, dam removal may also have negative short-term or potentially-permanent impacts on biota, primarily due to increased transport

and deposition of sediments previously retained behind the dam that can smother food sources, destroy spawning grounds, and disrupt existing assemblage structure (Burdick & Hightower, 2006; Gardner *et al.*, 2013; Shuman, 1995; Stanley & Doyle, 2003; Thomson *et al.*, 2005), or due to the introduction of novel species interactions (Marks *et al.*, 2010; Schroeder *et al.*, 2012).

A rare opportunity to study the ecological effects of multiple dam removals in the southeastern U.S. was presented with the removal of two small mainstem dams on Twelvemile Creek, in Pickens County, South Carolina. Twelvemile Creek is a tributary to a large artificial reservoir (Lake Hartwell) on the upper Savannah River system. Twelvemile Creek was extensively polluted with PCBs originating from a capacitor manufacturing plant from 1955-1975; the waste site and its receiving waters were listed with the EPA Superfund Program in 1990. As part of a settlement for damages caused by PCB contamination, a natural resources board of trustees facilitated the removal of two out of three mainstem dams on Twelvemile Creek. Dam removal began in August 2009 with the initial dredging behind the upper dam (Woodside I Dam); this dam was completely removed by April 2011. Dredging and removal preparations on the lower dam (Woodside II Dam) began in April 2011, and removal was completed in September 2011.

The primary objective of this study was to assess changes in the instream habitat and fish assemblage of Twelvemile Creek associated with the removal of two mainstem dams. We examined patterns in instream habitat, fish metrics, and fish assemblage structure before and after dam removals in order to evaluate the extent of habitat and biological impact, and to examine the process and timing of fish assemblage recovery.

Dam removal rates are expected to increase over time throughout the U.S., and this research should serve as a valuable tool for managers faced with questions and concerns regarding fish assemblage response.

Methods

Twelvemile Creek is located in the EPA level IV Inner Piedmont ecoregion of northwestern South Carolina, USA (Figure 3.1; Omernik, 1987). The small river drains a watershed of approximately 356 km² and is a major headwater tributary to Lake Hartwell, a 226 km² surface-area reservoir constructed between 1955 and 1964 by damming a portion of the upper Savannah River system. The Twelvemile Creek watershed is largely forested (55.6%) and pasture/shrubland (29.7%), with a relatively low level of urban development (12.4%) (SCDHEC, 2014). We established a study section in the lower portion of Twelvemile Creek that was approximately 7.25 km in length that encompassed three small run-of-the-river dams (Figure 3.1). The portion of this study section that contained all three dams is largely characterized by steep, gorge-like riparian terrain. The river's steep valley walls are lined with mountain laurel and rhododendron; such landscape and floral features are somewhat atypical of the surrounding Piedmont region. In contrast, the study section terrain further above and below all dams contains a gentle slope more typical of the region. The upstream-most dam (hereafter the 'Easley-Central Dam') is located approximately 5.1 km upstream of Lake Hartwell, has a hydraulic height of approximately 6 m, and retains a small impoundment that supplies drinking water to a local water district (Bechtel Engineering Inc., 1994). The next two downstream-most dams (Woodside I Dam and Woodside II Dam) were built in 1937 and

1895 respectively, and both were associated with hydromechanical and hydroelectric power production for the now abandoned Norris Cotton Mill in Cateechee, SC. The Woodside I Dam had a hydraulic height of 9.4 m and was located approximately 4 km upstream of Lake Hartwell, and the Woodside II Dam had a hydraulic height of 13 m and was located approximately 2.4 km upstream of Lake Hartwell. Each of the Woodside Dams retained small impoundments that were approximately 40 m wide and 60-90 m in length.

Sampling Design

We utilized a modified Before-After-Control-Impact (BACI) sampling design (Underwood, 1992; Underwood, 1994). We established six sampling sites of approximately 150 m in length to collect biological and habitat data (Figure 3.1). The sampling sites were distributed as follows: 1) an alluvial undisturbed reference reach located upstream of both Woodside Dams, and 2.0 km upstream of the uppermost Easley-Central Dam (Upstream) 2) an impounded reach immediately upstream of the Woodside I Dam (Woodside I Above), 3) a bedrock-constrained free-flowing reach immediately downstream of the Woodside I Dam (Woodside I Below), 4) an impounded reach immediately upstream of the Woodside II Dam (Woodside II Above), 5) a bedrock-constrained free-flowing stream reach immediately downstream of the Woodside II Dam (Woodside II Below), and 6) an alluvial reach located approximately 1.5 km downstream of the Woodside II Dam (Downstream). This study referenced ten biological and habitat samples collected across sites before and after dam removal, in the fall and spring seasons (December 2006, August 2009, April 2010, September 2010, April 2011,

October 2011, April 2012, October 2012, April 2013, and October 2013). The Woodside I Dam was removed in April of 2011, yielding 4 pre-removal and 6 post-removal samples. The Woodside II Dam was removed in September of 2011, yielding 5 pre-removal and 5 post-removal samples.

Habitat

We recorded depth (m), velocity (m/s), and inorganic substrate particle size (mm) at a representative point within each of twenty sampled stream segments per sample site (see fish collection for segment details). Depth and velocity were measured using a Marsh-McBirney Model 2000 Flo-Mate portable flowmeter and top-setting wading rod, and measured values were site-averaged for statistical analyses. Inorganic substrates were measured in millimeters at the intermediate axis, and median inorganic particle size (D50) was calculated for each site. Inorganic substrates considered to be bedrock were recorded as 999 mm, a standardized upper inorganic particle size limit. We measured wetted-width (m) at 5 transects spaced evenly across each sample site reach, and a site-averaged width was calculated. Turbidity was recorded using a MicroTPWTM turbidimeter (NTU). Water temperature, dissolved oxygen, conductivity, and pH were recorded prior to fish sampling using a YSI 556 MPSTM multiparameter probe, but none of these measurements were included in subsequent reported analyses due to low variability among sites and across time.

Fish

We collected fishes with a standardized electrofishing effort within each of our six sample sites. Twenty seine-set collections, each covering a stream segment area of

approximately 15m², were obtained in the following manner: a single backpack electrofisher operator (Smith-Root Model LR-24) acted in synchrony with one-two persons that collected fish with dipnets, all kicking downstream towards two persons holding a 3m seine. All fishes encountered per seine-set were collected, field identified to species level, recorded, and released after the twenty seine-sets at a site were completed. We preserved and returned specimens with any uncertainties in identification to the lab.

Statistical Analyses

A combination of univariate analyses of fish assemblage metrics and multivariate ordination was used to evaluate fish assemblage and instream habitat response to multiple dam removals on Twelvemile Creek. We used a replicated Before-After (BA) analysis to test for the effects of dam removal on instream habitat parameters. We calculated site-averaged values for both velocity (m/s) and depth (m), and calculated median particle size (mm) and turbidity (NTU). We tested for differences in instream habitat parameters before and after dam removal per sample site, and tested for differences between sites immediately upstream and downstream of dams both before dam removal and after dam removal. Habitat data were log-transformed as necessary to meet homogeneity of variances requirements of BA analyses. We considered the effect of dam removal to be significant if a given site displayed significant differences in habitat before versus after dam removal, or if sites immediately upstream and downstream of each dam showed differences prior to dam removal, then similarities after dam removal.

We additionally used a replicated BA analysis to examine the effects of dam removal on several often-reported fish assemblage metrics: total density, taxa richness,

benthic invertivore density, insectivorous cyprinid density, round-bodied sucker density, native centrarchid density, and non-native density. Densities were calculated as number of individuals per seine-set, out of a total of 20 seine-sets. We tested for differences in metrics before and after dam removal within sample sites, and tested for differences between sites immediately upstream and downstream of dams both before dam removal and after dam removal. Fish metrics were log-transformed as necessary to satisfy homogeneity of variances requirements. The effect of dam removal was considered significant if a given site displayed differences in a fish metric before and after dam removal, or if sites immediately upstream and downstream of each dam showed differences prior to dam removal, then similarities after dam removal. Preliminary analysis revealed that non-native density lacked a normal distribution despite transformation efforts, therefore we plotted non-native density by site over time to visually highlight patterns in non-native fish density before and after dam removal and provide further insight into assemblage changes among sites.

We performed non-metric multidimensional scaling (NMDS) on a species relative abundance matrix to examine changes in fish assemblage abundance structure before and after dam removal, and to assess how assemblage structure was related to measured instream habitat parameters (Clarke, 1993; Kruskal, 1964). Prior to analysis, we removed 12 species whose abundances comprised less than 5% of total collections and were identified as strongly influencing the analysis based on rarity alone (Lohr & Fausch, 1997; Matthews & Marsh-Matthews, 2011). The majority of these species were seasonal migrants from Lake Hartwell, others were represented by single individuals, or were

multiple individuals captured at only one site on only one occasion. The final relative abundance matrix contained 25 species. We applied a double-root transformation to reduce the effect of large differences in fish abundances among samples. NMDS was performed in R's vegan package (R Core Development Team, 2012) using the Bray-Curtis distance measure (Bray & Curtis, 1957), a random starting configuration, and 1000 runs with real data. We used a Monte-Carlo test with 20 iterations and 10 randomized runs to determine the probability of obtaining an equal or lower stress value by chance ($\alpha = 0.05$). We used Pearson correlation analysis to link instream habitat variables with our NMDS solution; habitat variables were log-transformed prior to this analysis.

Results

Before-After Analyses: Habitat

The bulk of expected habitat changes in former impounded sites (Woodside I Above, Woodside II Above) occurred rapidly after dam removal, as the lentic habitats transformed to lotic habitats and became increasingly similar to the habitat conditions found in their respective downstream counterparts (Woodside I Below, Woodside II Below). Prior to dam removal, both of the small impoundments upstream of the Woodside I and II Dams had slower velocities, smaller median inorganic particle sizes (low D50 – dominantly sand), and were wider than their respective downstream free-flowing counterparts (all $P < 0.05$, Table 3.1). After dam removal, the average velocities and median substrate sizes of both Woodside I Above and Woodside II Above increased dramatically in comparison to their prior impounded conditions (both $P < 0.05$, Table 3.1), and became similar to the velocity and substrate conditions found in their respective

downstream free-flowing counterparts (both $P > 0.05$, Table 3.1). The average widths of the impoundments at Woodside I Above and Woodside II Above were both greater than the average widths of their respective downstream free-flowing counterparts prior to dam removal (both $P < 0.05$, Table 3.1). The former impounded area at Woodside I Above remained wider than its downstream free-flowing counterpart after dam removal ($p = 0.01$), whereas the average width of Woodside II Above decreased after dam removal ($p = 0.01$), and became more similar in width to its downstream free-flowing counterpart ($p = 0.37$). We found no significant differences in average depths and turbidities at Woodside I Above or Woodside II Above before and after dam removal (all $P > 0.05$, Table 3.1).

Unlike the dramatic habitat changes we observed in both former impoundments following dam removal, we found no significant differences in any of the habitat measurements before and after dam removal at sites immediately below dams (Woodside I Below, Woodside II Below), or at the Upstream and Downstream sites (all $P > 0.05$, Table 3.1). We did visually observe a marked increase in fine sediment deposition at both Woodside I Below and Woodside II Below after both dam removals, although our BA analysis did not reveal these changes. The fresh sediments were likely derived from fine sediments previously trapped behind the dams, and deposition appeared to be greater at Woodside II Below than at Woodside I Below. Fresh sediments were also observed at the Downstream site, although this change was also not statistically significant. Prior to dam removal, the dominant median inorganic particle size at the Downstream site was coarse

sand (median = 4.5mm), but converted to fine sand (median = 0.5mm) after dam removal.

Before-After Analyses: Fish

We captured 11,117 individual fish comprised of 37 species and 8 families over the course of this study. The BA analyses of our fish assemblage metrics, detailed below, indicated that fish assemblages immediately above (Woodside I Above, Woodside II Above) and below (Woodside I Below, Woodside II Below) both dams displayed significant changes in assemblage structure associated with dam removal. In contrast, we found no significant changes in fish assemblage metrics at the Upstream and Downstream sites, indicating no measured impact of dam removal on the fish assemblages of those sample locations.

Woodside I Above, Pre v. Post

All metrics, except richness, that were calculated for the impoundment above the Woodside I Dam differed before and after dam removal (all $P < 0.05$, Table 3.2). Total density, benthic invertivore density, insectivorous cyprinid density, and round-bodied sucker density was increased after dam removal, and native centrarchid density was decreased after dam removal.

Woodside I Below, Pre v. Post

Total density, richness, insectivorous cyprinid density, round-bodied sucker density, and native centrarchid density at the free-flowing site immediately downstream the Woodside I Dam did not differ before and after dam removal (all $P > 0.05$, Table

3.2). However, benthic invertivore density was decreased after dam removal ($P = 0.02$), potentially indicating a downstream benthic disturbance following dam removal.

Woodside I Above v. Woodside I Below, Pre v. Post

All fish metrics, except richness, differed between the sites immediately upstream and immediately downstream of the Woodside I Dam prior to dam removal (all $P < 0.05$, Table 3.2). Total density, benthic invertivore density, insectivorous cyprinid density, and round-bodied sucker density were greater, and native centrarchid density was less in the free-flowing site immediately downstream the Woodside I Dam than in the impounded site immediately upstream. After dam removal, all metrics that showed differences between sites immediately upstream and downstream of the Woodside I Dam before dam removal, were found statistically similar (all $P > 0.05$, Table 3.2). These findings suggest the fish assemblage of the former impoundment showed a recovery in total density, insectivorous cyprinid density, round-bodied sucker density, and native centrarchid density to the expected pre-removal baseline conditions established at Woodside I Below. Although benthic invertivore density increased in the former impoundment after dam removal, and was found to be similar to post-removal downstream benthic invertivore densities, it did not eclipse the baseline benthic invertivore densities established at the downstream free-flowing site prior to dam removal. This indicates a lingering benthic dam removal disturbance at both Woodside I Above and Woodside I Below.

Woodside II Above, Pre v. Post

We observed a similar, yet less consistent set of responses among fish metrics measured at sites immediately above and below the Woodside II Dam. Of the metrics

calculated for the impoundment above the Woodside II Dam, only benthic invertivore density and native centrarchid density differed before and after dam removal (both $P < 0.05$, Table 3.2). Benthic invertivore density was increased and native centrarchid density was decreased in the former impoundment after dam removal. We found no changes in total density, richness, insectivorous cyprinid density, or round-bodied sucker density after dam removal.

Woodside II Below, Pre v. Post

Total density, richness, benthic invertivore density, and native centrarchid density differed before and after dam removal at the free-flowing site immediately downstream of the Woodside II Dam (all $P < 0.05$, Table 3.2), while insectivorous cyprinid density and round-bodied sucker density did not differ before and after dam removal (both $P > 0.05$, Table 3.2). Total density, richness, benthic invertivore density, and native centrarchid density all significantly decreased after dam removal, potentially indicating a downstream impact due to dam removal.

Woodside II Above v. Woodside II Below, Pre v. Post

Total density, benthic invertivore density, and insectivorous cyprinid density differed between the sites immediately upstream and downstream of the Woodside II Dam before dam removal (all $P < 0.05$, Table 3.2). Each of these metrics was higher in the free-flowing site below the Woodside II Dam, and lower in the impounded area above the dam prior to dam removal. Richness, round-bodied sucker density, and native centrarchid density did not differ at sites above and below the Woodside II Dam prior to dam removal (all $P > 0.05$, Table 3.2). After dam removal, total density, benthic

invertivore density, and insectivorous cyprinid density increased in the former impoundment (Woodside II Above), and became similar to densities observed in post-removal Woodside II Below (All $P > 0.05$, Table 3.2). Cumulatively, these findings suggest that several aspects of fish assemblage structure at Woodside II Below remained negatively impacted at 2-years post-removal of the Woodside II Dam, and also suggest that Woodside II Above has not shown all expected assemblage changes anticipated with dam removal. We found that total density, benthic invertivore density, insectivorous cyprinid density were less in the impoundment as compared to densities in the downstream free-flowing site prior to dam removal, and these metrics were found to be similar in both sample locations after dam removal. However, after dam removal, benthic invertivore densities and total densities of both Woodside II Above and Woodside II Below failed to reach the expected baseline conditions set at Woodside II Below prior to dam removal. In contrast, cyprinid densities appeared to have recovered to pre-dam removal levels at both Woodside II Above and Woodside II Below.

Non-Native Density

Prior to both dam removals, non-native density was minimal among sites, and no non-native species were captured at sites above the lower-most dam (Woodside II Dam; Figure 3.2). All pre-dam removal non-native captures were represented by a single species, *Pylodictis olivaris*. We did not observe an increase in non-native density after the removal of the Woodside I Dam. However, at 1-month after the removal of the downstream-most Woodside II Dam, non-native species density increased sharply at both Woodside II Below and Woodside II Above, as well as at the Downstream site. This

increase reflected the presence of *Pylodictis olivaris* in greater numbers than captured previously, and an increase in *Micropterus henshalli*, a species that had never been captured in any of our samples prior to dam removal. At 6-months post- removal of the Woodside II Dam, we had captured *Micropterus henshalli* at Downstream, Woodside II Below, Woodside II Above, as well as the free-flowing site immediately downstream of the former upper dam (Woodside I Below). Further fish surveys showed captures of *Micropterus henshalli* at Woodside I Above. In contrast, we did not capture *Micropterus henshalli* in our Upstream reference site, located above the third dam (Easley-Central Dam) that remained on the river. We captured the majority of *Micropterus henshalli* ($N = 9$) within 1- year of the removal of the lower-most dam (Woodside II Dam), and observed only one additional catch occurrence between 1- and 2- years. To date, we have not reinforced our visual identifications of *Micropterus henshalli* with genetic verifications, although genetic samples were taken from almost all non-native fish captured.

Non-Metric Multidimensional Scaling

The NMDS resulted in a 2-dimensional solution that explained 97.5% of the variation in the fish relative abundance matrix, and resulted in a final stress value of 15.67, a final instability of 0.0098, and a Monte Carlo test indicated significance at $p < 0.001$. The NMDS solution confirmed that differences in assemblage structure among sites were strongly correlated to changes in habitat conditions before and after dam removal, showed that assemblages varied longitudinally across sample sites (i.e. assemblages displayed upstream-downstream variation), and provided insight into the gradual temporal changes in assemblage structure succeeding dam removal (Figure 3.3).

Prior to dam removal, the habitat conditions and fish assemblage structure of both impoundments (Woodside I Above, Woodside II Above) were similar. The impoundments contained sand-dominated substrates (low D50), slow velocities and large average widths, and were characterized by lentic species such as *Lepomis auritus*, *Lepomis gulosus*, *Lepomis macrochirus*, *Lepomis microlophus*, and *Micropterus salmoides*. The NMDS solution also revealed similarities in the habitat conditions and assemblage structure of both free-flowing sites (Woodside I Below, Woodside II Below) prior to dam removal. The free-flowing sites had higher average velocities and much larger median substrate sizes than the impounded sites, and were characterized by lotic species such as *Ameiurus brunneus*, *Etheostoma inscriptum*, *Hybopsis rubrifrons*, *Hypentelium nigricans*, *Notropis hudsonius*, *Noturus insignis*, and *Notropis lutipinnis*. The fish assemblages of the free-flowing sites showed upstream-downstream longitudinal variation, where the free-flowing site below the Woodside I Dam (Woodside I Below) was more similar to the Upstream assemblage through time, and the free-flowing site below the Woodside II Dam (Woodside II Below) was more similar to the Downstream assemblage through time.

After the first dam removal (Woodside I Dam), the fish assemblage structure of its former upstream impoundment (Woodside I Above) showed a dramatic drop in total numbers of all species at 1-month post-removal, but the general assemblage structure became similar to its immediate downstream free-flowing counterpart (Woodside I Below) and the free-flowing site below the lower dam (Woodside II Below) by approximately 6-months after dam removal. At 6-months post-removal, we observed

relatively strong increases in *Percina nigrofasciata*, *Etheostoma inscriptum*, *Nocomis leptocephalus*, *Hybopsis rubrifrons*, *Notropis lutipinnis*, *Hypentelium nigricans*, and *Ameiurus brunneus*, and dramatic reductions in *Lepomis macrochirus*, *Lepomis auritus*, and *Micropterus salmoides*. The downstream free-flowing site below the former impoundment (Woodside I Below) showed little variation in assemblage structure after the removal of the Woodside I Dam, indicating minimal impact of dam removal to the fish assemblage of this site.

Workers began work to remove the second, downstream-most dam (Woodside II Dam) immediately following the Woodside I Dam removal, and completed its removal within five months. After its removal, the fish assemblage structure of the former impoundment (Woodside II Above) showed a noteworthy decrease in total numbers and species in our 1- and 6-months post-removal samples. We observed immediate dramatic reductions in *Lepomis macrochirus*, *Lepomis auritus*, and *Lepomis cyanellus*, and captured a sparse mix of lentic (*Micropterus salmoides*, *Micropterus henshalli*) and several lotic species (*Percina nigrofasciata*, *Hypentelium nigricans*, *Ameiurus brunneus*, *Notropis hudsonius*, *Micropterus coosae*) for up to 1-year following dam removal. The fish assemblage of this former impoundment came to resemble the assemblage structure of its downstream free-flowing counterpart (Woodside II Below), the free-flowing site below the Woodside I Dam, and the former impounded area above the removed upper dam (Woodside I Above) in approximately 1 – 1.5 years after the removal of the Woodside II Dam.

Whereas the NMDS revealed minimal impact on the free-flowing assemblage below the Woodside I Dam following dam removal, we did observe an impact on the free-flowing assemblage below the Woodside II Dam immediately following its removal. We observed a striking decrease in total numbers, and an immediate absence of *Percina nigrofasciata*, *Cyprinella nivea*, *Etheostoma inscriptum*, *Nocomis leptocephalus*, *Hypentelium nigricans*, *Notropis hudsonius*, *Notropis lutipinnis*, *Lepomis macrochirus*, *Micropterus coosae*, *Lepomis cyanellus*, and *Lepomis microlophus* from the sample at 1-month post dam removal. Concurrently, we observed an increase of *Ictalurus punctatus*, as well as *Pylodictis olivaris* and *Micropterus henshalli*, two non-native species never captured at the site previously. Several individual fish showed bacterial infections and lesions. However, the NMDS indicated that the assemblage structure of this site became similar to the other free-flowing sites at approximately 1 -year after dam removal, indicating a relatively quick structural recovery.

Discussion

We observed changes in habitat, fish metrics, and abundance structure at sample sites immediately above (Woodside I Above, Woodside II Above) and below (Woodside I Below, Woodside II Below) each dam after dam removal. The bulk of in-stream habitat adjustments and fish assemblage changes occurred within the first year of each individual dam removal. Lotic habitats quickly reestablished following major geomorphic channel adjustments, and previously lentic-dominated fish assemblages of former impoundments generally shifted to a lotic-dominated structure. Despite these prominent assemblage shifts, we found only a partial recovery in benthic invertivore density at Woodside I

Above, and decreased benthic invertivore density at Woodside I Below at 2.5-years post dam removal. We found the negative biological impacts of the second dam removal (Woodside II Dam) more severe, with only a partial recovery in total density and benthic invertivore density at Woodside II Above, and decreased total density, richness, benthic invertivore density, and native centrarchid density at Woodside II Below at 2-years. Non-native density increased sharply within all sample locations below the remaining 3rd dam (Easley-Central Dam) for approximately 1-year after the removal of the lowermost Woodside II Dam. This increase was driven primarily by captures of *Micropterus henshalli*, an introduced species common in Lake Hartwell, but not captured in any Twelvemile Creek pre-dam removal samples.

We found no significant habitat or fish assemblage changes at our Upstream reference or the Downstream site, indicating that a) observed changes were constrained to the high-gradient ~2.7 km river reach that contained the two dams, and b) changes in the high-gradient reach were responses to the impacts of dam removal rather than natural fluctuations or a secondary disturbance event. The Upstream and Downstream sites did help us discern spatial variation in assemblage structure. Prior to dam removal, our NMDS indicated that the free-flowing assemblages in the lower river reaches (Downstream, Woodside II Below) showed differences in species composition and abundances as compared to free-flowing assemblages in the upper river reaches (Upstream, Woodside I Below). Such upstream-downstream assemblage patterns are common to riverine fishes (Danehy *et al.*, 1998; Fausch, Karr & Yant, 1984; Sheldon, 1968; Vannote *et al.*, 1980), and have been documented on rivers of similar size in the

Piedmont region of South Carolina (Kubach, Scott & Bulak 2011). The two impounded sites (Woodside I Above, Woodside II Above) showed no adherence to this upstream-downstream pattern prior to dam removal, indicating that habitat alterations caused by the Woodside Dams dictated observed assemblage patterns and disrupted the natural longitudinal fish assemblage structure (Araujo, Pinto & Teixeira, 2009). The removal of both Woodside Dams successfully restored longitudinal fish assemblage structure among formerly impounded sites, as their habitats and assemblages became more similar to their neighboring free-flowing counterparts.

Effects of Dam Removals on Instream Habitat

Prior to dam removal, both impoundments (Woodside I Above, Woodside II Above) were shallow, with slow laminar flows, a fine sand benthos, and no large inorganic substrates characteristic of the free-flowing sites below dams. These homogenous habitat conditions were created by years of fine sediment accumulation behind the Woodside Dams. After dam removal, we observed major geomorphic channel adjustments in former impoundments which created a heterogeneous riffle-run flow pattern and an increase in larger gravel/cobble/boulder/bedrock substrates; habitat conditions similar to downstream free-flowing sites and endemic to the high-gradient reach containing the two former dams (Whitener, 2013).

Although we found dramatic habitat changes in both former impoundments after dam removal, we detected no significant habitat changes in either downstream free-flowing site (Woodside I Below, Woodside II Below). These findings were in discord with our field observations, which indicated increased suspended sediment during and

immediately after each dam removal, and increased downstream fine sediment deposition that attenuated over time, but persisted for the duration of this study. These findings are additionally in discord with other dam removal studies, which have predominantly found that benthic habitats downstream of dam removals are impaired, at least temporarily, due to the downstream flushing of impoundment and upstream sediments (Gardner *et al.*, 2013; Stanley & Doyle, 2003; Thomson *et al.*, 2005). Regardless, we were able to identify a handful of studies that cited increased sediment flux after dam removal, but also failed to successfully quantify sediment transport and deposition rates (Hart *et al.*, 2002; Kanehl & Lyons, 1997; Pollard & Reed, 2004; Winter, 1990).

Dam removal engineers removed approximately 152,900 m³ of sediment from the impoundments immediately upstream of both Woodside Dams prior to dam removal, and transported it to an off-site sediment management unit. Despite this effort, residual fine sediments that heavily lined the riverbanks for 800-1000 m upstream of each dam were washed downstream over the course of this study. After the removal of the Woodside I Dam, an upstream headcut developed within several days that reached just downstream of the Easley-Central Dam. High-water storm events in 2012-2013 coupled with the restored high gradient channel quickly flushed the bulk of residual upstream sediment through the former Woodside I Above impoundment and Woodside I Below within ~6-12 months after dam removal. Downstream sediment flushing was decelerated by the presence of the Woodside II Dam, which captured much of the fine sediment from the Woodside I Dam removal. The Woodside II Dam was removed within 5-months of the Woodside I Dam, and during the removal process we observed dramatically elevated

suspended and deposited sediment levels not present with the Woodside I Dam removal. Elevated suspended sediments dissipated within ~ 1-month of dam removal, and the bulk of deposited sediments flushed through Woodside II Above and Woodside II Below within 1-1.5 years.

Effects of Dam Removals on Fish

Theory suggests that higher gradient streams can flush sediments more quickly than lower gradient streams, leading to faster rates of geomorphic and habitat restoration, which in turn influences the timing and extent of biological recovery (Doyle *et al.*, 2005). Both Woodside Dams were located within a single high-gradient stretch of river, yet we found that the rate of fish assemblage recovery was faster, and the extent of negative assemblage impacts was less at sites flanking the Woodside I Dam than at sites flanking the Woodside II Dam. Our results suggested that the rate and extent of biological recovery at each of the Woodside Dams was likely mediated by the combined influence of river gradient and the cumulative amount of sediment stored upstream. The influence of gradient was approximately equal among all Woodside sites, yet we believe that the cumulative amount of sediment was greater at Woodside II Above and Woodside II Below after these two sites captured upstream sediment from the Woodside I Dam removal. We suggest that the cumulative impacts of multiple dam removals led to a greater breadth of negative impacts on Woodside II fish assemblages.

The obvious problem with our assertion regarding the cumulative negative assemblage impacts of multiple dam removals was our obvious lack of results indicating substrate size decreases at either Woodside I Below or Woodside II Below. However,

support for our argument lies in the fact that dam removals are known to negatively impact downstream biota, at least temporarily, due to the downstream transport of sediments (Poff & Hart, 2002; Shuman, 1995; Wood & Armitage, 1997). While our habitat analysis failed to reveal downstream substrate changes, we did find negative downstream biological impacts at both Woodside I Below and Woodside II Below following dam removal which coincided with our visual observations of increased fine sediment deposition. We found decreased benthic invertivore density at Woodside I Below, and decreased total density, richness, benthic invertivore density, and native centrarchid density at Woodside II Below after dam removal. These findings strongly suggested that the Woodside Dam removals did indeed create downstream habitat disturbances, most likely due to fine sediment deposition, which were more intense at Woodside II Below than Woodside I Below. Although dam removal is also known to decrease water quality (Nechvatal, 2004), and release stored contaminants (Bednarek, 2001; Chatterjee, 1997) in downstream reaches, we do not believe either of these factors accounted for the pattern of downstream biotic changes we observed over the course of this study. The vast majority of PCB contaminants had washed downstream to Lake Hartwell decades earlier, and a recent report indicated that the residual PCB mass represented only 0.12-0.22 % of the original contamination (CH2MHILL, 2012). Water quality parameters such as turbidity showed temporary increases during and immediately after dam removal, but these changes were temporary and unlikely to have long-term consequences (Whitener, 2013).

Although we observed dam-specific differences in the degree of fish assemblage recovery in former impounded areas, and in the severity of negative assemblage impacts in free-flowing sites downstream, our general observations of fish assemblage structural changes were similar to findings from previous dam removal studies (Bednarek, 2001; Doyle *et al.*, 2005; Gregory, Li & Li, 2002; American Rivers, 2002). We generally observed a shift from a lentic-dominated to lotic-dominated assemblage in both former impoundments (Woodside I Above, Woodside II Above), with decreases in native centrarchid densities at both former impoundments, and increases in benthic invertivore density at Woodside II Above, and increases in total density, benthic invertivore density, insectivorous cyprinid density, and round-bodied sucker density at Woodside I Above. This pattern generally reflects the findings of others which have shown decreases in tolerant species such as centrarchids, and increases in intolerant habitat specialists such as darters, catostomids, and insectivorous cyprinids in formerly impounded areas after dam removal (Catalano, Bozek & Pellett, 2007; Kanehl & Lyons, 1997). Both Woodside Dam removals quickly restored high-quality large substrates in former impoundments, and restored natural riffle-run sequences that have improved the habitat quality for benthic species such as darters, which prefer coarse substrates and fast moving water (Page, 1983). However, benthic-oriented taxa were also the most negatively affected in downstream free-flowing sites after dam removal. Increased fine sediment deposition is known to decrease the fitness, reproduction, and food sources for benthic fishes (Waters, 1995), and our study indicated that the recovery of benthic taxa densities may take more than 2.5 -years, even in high-gradient systems (Maloney *et al.*, 2008).

Our study indicated that our choice of statistical analyses, and which fish metrics we examine may influence our interpretation of the timing and extent of biological recovery after dam removal. Our NMDS analyses provided insight into the timing of the bulk of fish assemblage changes among sites after dam removal. The bulk of assemblage changes occurred at Woodside I Above within 6-months of the removal of the Woodside I Dam, and Woodside I Below showed negligible assemblage changes associated with dam removal. In contrast, the bulk of assemblage changes occurred at Woodside II Above within 1-1.5 years after the removal of the Woodside II Dam, and Woodside II Below exhibited dramatic assemblage changes, the bulk of which attenuated after 1-year. Multiple studies have cited the approximate 1-year timeframe as the post-dam removal duration to biological recovery in high-gradient systems (Catalano, Bozek & Pellett, 2007; Kanehl & Lyons, 1997; Sethi *et al.*, 2004; Stanley *et al.*, 2002), and our NMDS results generally supported this timeframe. However, our fish metric BA analyses revealed more detailed information and insight into the variation of species responses and timing to fish assemblage recovery. We found that certain metrics such as benthic invertivore density were more sensitive to dam removal than others (e.g. richness), and indicated a much longer timeframe of biological recovery than interpreted from our NMDS analysis (2.0-2.5 – years versus 0.5-1.5 – years). Catalano *et al.* (2007) and Maloney *et al.* (2008) similarly found that only a subset of metrics showed sensitivity to dam removal. A combination of taxonomic, functional, and assemblage level analyses may be required to discern the timing to recovery and full suite of impacts on fish assemblages resulting from dam removal.

Dam Removal and the Restoration of Aquatic Connectivity

A primary goal of dam removal is to restore aquatic connectivity. Dam removal assists vagile and migratory species by increasing the length of movement corridors and opening up critical habitats (Bowman, 2001; Catalano, Bozek & Pellett, 2007; Estes, Myers & Mantini, 1993; Hill, Long & Hardin, 1994; O'Donnell *et al.*, 2001; Shuman, 1995; Smith *et al.*, 2000; Winter, 1990). Fish whose movements were formerly obstructed by dams may begin to move into formerly impounded and blocked reaches within days after dam removal (Hart *et al.*, 2002). The removal of the two Woodside Dams on Twelvemile Creek restored aquatic connectivity within to the lower stretch of Twelvemile Creek, but also opened the river to Lake Hartwell, an artificial man-made reservoir. The lower-most dam on Twelvemile Creek (Woodside II Dam) was constructed in 1895 when the Savannah River System flowed unimpeded, and nearly 65 years prior to the construction of Lake Hartwell. Therefore, dam removal established a novel connection between two substantially different hydrological habitats that was unrepresentative of pre-dam(s) conditions.

Reservoirs have known impacts on riverine fish assemblages, including the extirpation of obligate lotic species (Martinez *et al.*, 1994), increased tolerant habitat generalists (Ruhr, 1957), and increased abundances of native and introduced piscivores (Gido, Schaefer & Falke, 2009; Martinez *et al.*, 1994). However, surprisingly little is known about the effects of southeastern reservoirs on fishes in upstream free-flowing tributary streams that are not directly altered by impoundment (Franssen & Tobler, 2013; Pringle, 1997). River and reservoir systems share a common water course, but offer

substantially different habitat conditions for biota. While reservoirs are not an absolute migratory barrier, they likely impart migratory resistance on many riverine fish species, who may find reservoir habitats unsuitable aquatic corridors for movement (Hudman & Gido, 2013; Skalski *et al.*, 2008). However, reservoirs are often favorable habitat corridors for native and introduced piscivorous fishes, which in turn serve as source populations and may increase densities in upstream free-flowing tributary habitats (Gido, Schaefer & Falke, 2009).

We observed a sharp increase in non-native species density beginning at 1-month after the removal of the downstream-most Woodside II Dam. This increase was driven by captures of *Micropterus henshalli* (Alabama spotted bass), a piscivorous non-native species which had never been captured in any of our samples prior to dam removal. Our capture pattern appeared to indicate that *Micropterus henshalli* migrated in an upstream direction from Lake Harwell into the newly restored Twelvemile Creek section, however may alternatively reflect problems with probability of detection (MacKenzie *et al.*, 2002). Regardless, this capture pattern persisted for approximately 1-year after the removal of the Woodside II Dam, and then attenuated over time. The upstream movement of spotted bass posed an ecological concern because *Micropterus henshalli* readily hybridize with and deplete the genetic integrity of *Micropterus coosae* (redestye bass), a fish native to water bodies of the Savannah River drainage (Bangs, 2011). The presence of *Micropterus henshalli* is well documented in the major reservoirs of the Savannah River, but little is known about their distribution in tributary systems. Prior to their removal, it is possible that the Woodside Dams acted as protective barriers to an upstream invasion of

Micropterus henshalli from Lake Hartwell. A third dam (Easley-Central Dam) remains on Twelvemile Creek and effectively blocks the upper reaches from the upstream movement of fish. To date, we have not genetically verified the capture of any pure strain *Micropterus henshalli* or hybrids above the Easley-Central Dam. Our study highlights the potential for dam removal to inadvertently open up rivers to non-native colonization of previously unavailable stream sections, an ecological hazard that may be particularly relevant in southeastern U.S. states, where artificial impoundments and reservoir density is high.

Our study demonstrates that dam removal can reverse many of the negative impacts that dams have on fish assemblages, primarily through the restoration of high-quality lotic habitats required by the native suite of riverine species. However, we also demonstrated that dam removal can have short-term ecological trade-offs, such as sediment impacts, that vary given the unique characteristics of the dam removal(s), underlying geomorphological conditions, and fish assemblage attributes (Poff & Hart, 2002; Stanley & Doyle, 2003). Regardless, we believe dam removal as a restoration tool is unlikely to have long-term negative impacts on fish assemblages in high-gradient southeastern U.S. systems, as populations are likely to recover once habitat disturbances and sediment loads are fully reduced (Thomson *et al.*, 2005), and if highly vulnerable or sensitive species are not at risk (Sethi *et al.*, 2004).

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Table 3.1. Pre- and post- dam removal mean values (\pm SE) of habitat variables among BA pairwise comparisons. Values in bolded italics indicate a significant difference from the BA analysis at $P < 0.05$.

Comparison	Average Depth	Average Velocity	D50	Average Width	Turbidity
US pre • US post	0.51(0.09) • 0.54(0.08)	0.34(0.117) • 0.35(0.10)	3.77(6.55) • 0.50(0.01)	19.00(1.21) • 18.43(1.25)	12.48(1.21) • 6.88(1.25)
WSI Above pre • WSI Above post	0.41(0.16) • 0.50(0.05)	<i>0.11(0.06) • 0.42(0.08)</i>	<i>2.98(3.51) • 481.42(451.89)</i>	42.50(3.53) • 33.18(6.35)	7.77(4.12) • 6.22(1.81)
WSI Below pre • WSI Below post	0.49(0.05) • 0.51(0.03)	0.39(0.11) • 0.36(0.06)	279.65(208.46) • 388.41(342.73)	22.85(4.08) • 22.95(3.74)	10.52(5.01) • 6.743(1.86)
WSI Above pre • WSI Below pre	0.41(0.16) • 0.49(0.05)	<i>0.11(0.06) • 0.39(0.11)</i>	<i>2.98(3.51) • 279.65(208.46)</i>	<i>42.50(3.53) • 22.85(4.08)</i>	7.77(4.12) • 10.52(5.02)
WSI Above post • WSI Below post	0.50(0.05) • 0.51(0.03)	0.42(0.08) • 0.37(0.06)	481.41(451.89) • 388.41(342.73)	<i>33.18(6.35) • 22.95(3.75)</i>	6.22(1.81) • 6.74(1.86)
WSII Above pre • WSII Above post	0.44(0.09) • 0.49(0.04)	<i>0.14(0.07) • 0.42(0.05)</i>	<i>0.57(0.16) • 248.80(302.23)</i>	<i>40.30(11.38) • 19.10(4.25)</i>	12.86(11.38) • 6.59(4.25)
WSII Below pre • WSII Below post	0.46(0.06) • 0.46(0.07)	0.43(0.06) • 0.43(0.05)	320.79(171.51) • 277.05(277.19)	22.41(2.23) • 21.10(2.57)	10.83(4.52) • 6.75(0.60)
WSII Above pre • WSII Below pre	0.44(0.09) • 0.46(0.06)	<i>0.14(0.08) • 0.43(0.06)</i>	<i>0.57(0.16) • 320.79(171.51)</i>	<i>40.30(11.38) • 22.41(2.23)</i>	12.86(7.31) • 10.83(4.53)
WSII Above post • WSII Below post	0.49(0.04) • 0.46(0.07)	0.41(0.05) • 0.43(0.04)	248.80(302.80) • 277.05(277.19)	19.10(4.25) • 21.10(2.57)	6.59(1.56) • 6.75(0.60)
DS pre • DS post	0.48(0.06) • 0.44(0.06)	0.32(0.03) • 0.35(0.07)	4.81(4.01) • 0.50(0.0)	24.48(5.39) • 27.57(4.47)	7.99(3.44) • 8.05(2.06)

Table 3.2. Pre- and post- dam removal mean values (\pm SE) of fish metrics among BA pairwise comparisons. Values in bolded italics indicate a significant difference from the BA analysis at $P < 0.05$.

Comparison	Total Density	Richness	Benthic Invertivore Density	Insectivorous Cyprinid Density	Round-Bodied Sucker Density	Native Centrarchid Density
US pre • US post	4.96(1.09) • 3.85(2.16)	11.25(1.25) • 12.50(1.04)	1.85(1.40) • 0.5(0.35)	0.86(0.64) • 1.71(1.4)	0.5(0.31) • 0.42(0.24)	0.51(0.33) • 0.39(0.14)
WSI Above pre • WSI Above post	<i>2.22(1.02) • 10.24(7.62)</i>	7.5(2.12) • 10.5(3.02)	<i>0.03(0.035) • 1.75(1.45)</i>	<i>0.4(0.56) • 3.44(2.52)</i>	<i>0.18(0.25) • 2.61(2.19)</i>	<i>2.95(0.49) • 0.12(0.16)</i>
WSI Below pre • WSI Below post	12.98 (1.58) • 10.19(5.63)	14.5(0.58) • 13.8(3.43)	<i>4.43(1.61) • 2.00(0.96)</i>	3.59(0.88) • 3.53(2.48)	1.73(0.66) • 1.48(1.22)	0.51(0.30) • 0.37(0.42)
WSI Above pre • WSI Below pre	<i>2.23(1.02) • 12.98(1.58)</i>	7.5(2.12) • 14.5(0.58)	<i>0.03(0.04) • 4.44(1.61)</i>	<i>0.40(0.56) • 3.59(0.88)</i>	<i>0.17(0.25) • 1.73(0.66)</i>	<i>2.95(0.49) • 0.51(0.30)</i>
WSI Above post • WSI Below post	10.24(7.62) • 10.19(5.63)	10.5(3.02) • 13.83(3.43)	1.75(1.46) • 2.00(0.96)	3.44(2.52) • 3.53(2.48)	2.61(2.19) • 1.48(1.22)	0.12(0.16) • 0.36(0.42)
WSII Above pre • WSII Above post	5.70(3.17) • 4.19(2.73)	11.00(3.37) • 11.4(1.67)	<i>0.04(0.05) • 0.54(0.31)</i>	0.74(0.62) • 2.3(2.7)	0.24(0.27) • 0.33(0.14)	<i>2.11(0.90) • 0.21(0.22)</i>
WSII Below pre • WSII Below post	<i>18.85(7.2) • 5.27(2.18)</i>	<i>14.4(1.67) • 11.00(1.58)</i>	<i>2.42(0.99) • 0.93(0.69)</i>	8.63(8.73) • 3.04(1.70)	0.41(0.20) • 0.27(0.27)	<i>5.95(6.61) • 0.09(0.04)</i>
WSII Above pre • WSII Below pre	<i>5.70(3.17) • 18.85(7.20)</i>	11.0(3.37) • 14.4(1.67)	<i>0.04(0.05) • 2.4(0.99)</i>	<i>0.74(0.62) • 8.63(8.73)</i>	0.24(0.28) • 0.41(0.20)	2.11(0.90) • 5.95(6.61)
WSII Above post • WSII Below post	4.19(2.73) • 5.27(2.17)	11.4(1.67) • 11.0(1.58)	0.54(0.31) • 0.93(0.69)	2.31(2.72) • 3.04(1.70)	0.33(0.14) • 0.27(0.27)	0.21(0.22) • 0.09(0.04)
DS pre • DS post	11.99(6.81) • 9.14(4.08)	14.2(2.17) • 13.4(3.85)	0.80(0.56) • 0.38(0.19)	6.77(4.42) • 6.21(1.25)	0.54(0.54) • 0.14(0.09)	2.27(1.14) • 1.84(2.58)

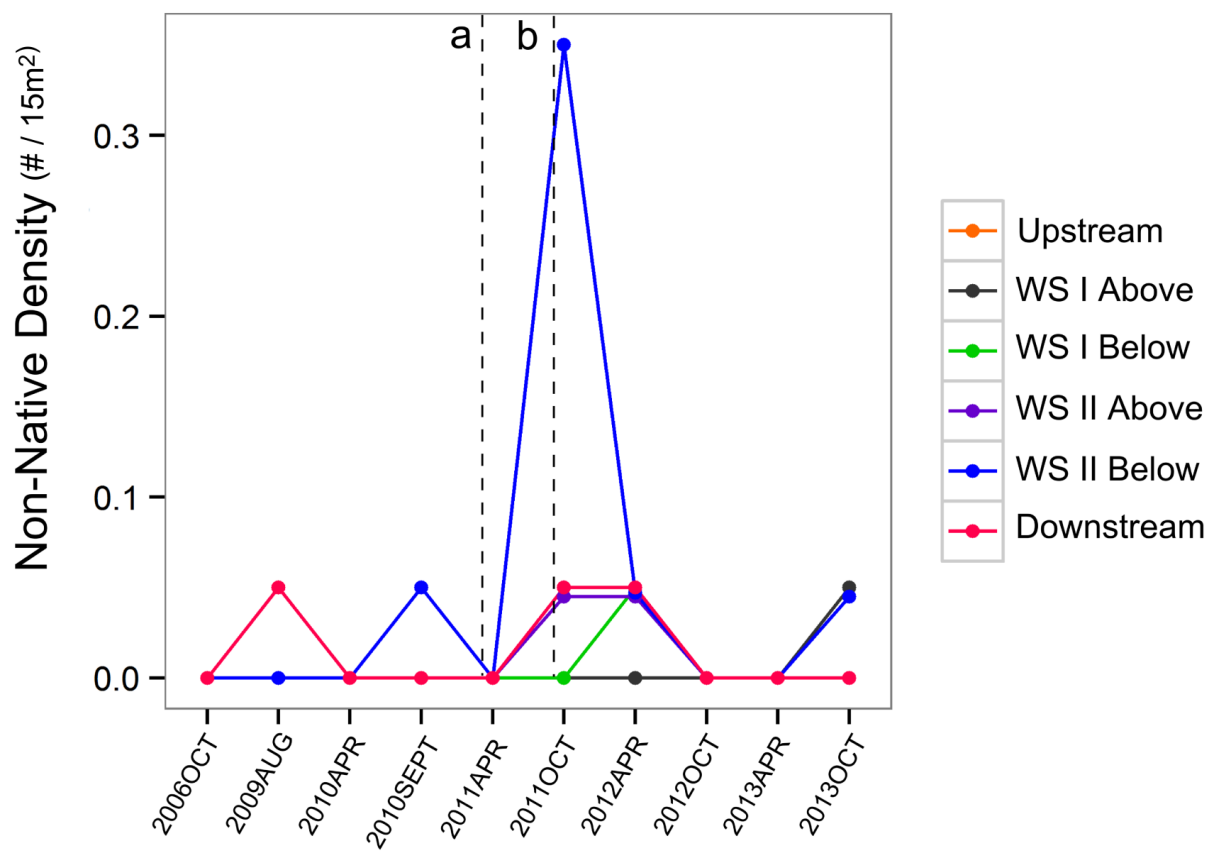


Figure 3.2. Changes in non-native fish density across all study sites over the 7-year study period. Vertical dashed lines indicate removals of the a) Woodside I Dam, and the b) Woodside II Dam.

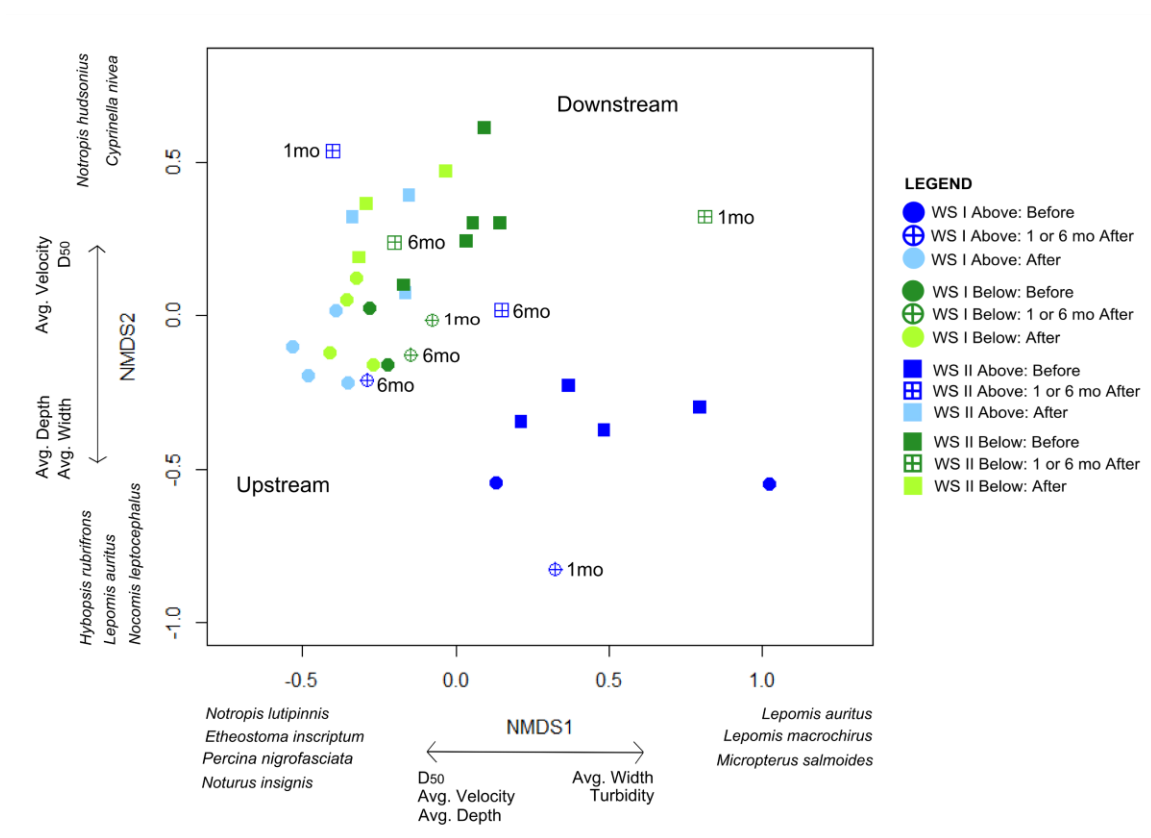


Figure 3.3. Non-Metric Multidimensional Scaling (NMDS) ordination of fish assemblages by site. Points closer to one another in the ordination are more similar in assemblage structure. Upstream and Downstream coordinates are not shown but fall tightly around locations indicated by ‘Upstream’ and ‘Downstream’. Species names along axes refer to species that correlate strongly on each axis, whether positively or negatively. Habitat variables under arrows are parameters that were strongly correlated with each NMDS axis. Species correlations were inherent weights (i.e. the ordination is based on the species), whereas habitat correlations were post-hoc calculations.