INFLUENCE OF DROUGHT ON SEASONAL FISH ASSEMBLAGES AND HABITAT IN THE LOWER FLINT RIVER BASIN, GEORGIA

by

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Under the Direction of James T. Peterson

ABSTRACT

Seasonal fish assemblages and their habitats were examined in the lower Flint River Basin during the drought years of 2001 and 2002 and the non-drought year of 2003. Species richness, biomass, and Index of Biotic Integrity were lower during the drought years, which suggested that low streamflows had negative effects on the fish assemblages. Fishes were able to recolonize drought-affected streams presumably by large-scale, seasonal movements of adult and juvenile fish. Species richness and biomass also were higher in groundwater-dominated streams during winter and summer, which suggests that these streams function both as winter thermal refugia and as significant fish production areas throughout the year. Findings from this study suggest that stream fragmentation could limit natural recolonization of impacted stream reaches and that lower Flint River Basin aquatic biota would benefit from management decisions based on streamflow models that incorporate both spatial and temporal components for evaluating long-term effects of flow policies.

INDEX WORDS: Drought, Flint River Basin, Seasonal Fish Assemblages, Groundwater, Fragmentation, Akaike Information Criteria

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DEDICATION

This thesis is dedicated to the memory of my grandfather, J. W. McCargo, who passed away while I was pursuing this degree. During his lengthy battle with a debilitating illness, he displayed enduring courage and resolve. His example is a constant reminder that all things can be accomplished with dedication, hard work, and faith.

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CHAPTER 1

INTRODUCTION

Lotic ecosystems in the southeastern United States contain the richest fish fauna in North America north of Mexico (Warren and Burr 1994; Warren et al. 2000). At least 25% of the 790 native freshwater fish species that occur throughout the entire United States are found in the Southeast, and 7 of the 11 southeastern states contain more species than any other state in the country (Warren and Burr 1994). The Southeast also contains the largest number of endemic fish species in the country, with at least 40 species occurring in the Mobile basin, 33 in the Tennessee River drainage, 10 in the Cumberland River drainage, and 9 in the Roanoke-James River drainage (Warren and Burr 1994; Warren et al. 2000). Because of its diverse and endemic fish fauna, the Southeast is often considered an ecologically significant “hotspot” of biodiversity (Lydeard and Mayden 1995).

Southeastern lotic ecosystems also contain a very high proportion of imperiled fish species at risk of extinction (Warren and Burr 1994; Lydeard and Mayden 1995; Warren et al. 2000). Approximately 28% of the known native fish species in the Southeast are extinct, endangered, threatened, or vulnerable, and more species are classified as endangered each year (Warren et al. 2000). The demise of many native southeastern fish species has largely been attributed to habitat loss and alteration such as stream channelization, impoundment, chemical pollution, and sedimentation. The demise also is associated with poor land management practices and increased urbanization (Tabit and Johnson 2002). Over the last decade, human population growth in the Southeast was well above the national average and was as high as 26% in Georgia (U.S. Census Bureau 2000). This increased population growth probably is placing additional demands on water resources. Because of the current status and increasing rate of imperilment, previous studies suggest that southeastern fishes may be on the brink of an extinction crisis unless improvements are made in large-scale management of land and water resources (Warren and Burr 1994; Warren et al. 2000).

The Southeast also is susceptible to severe drought conditions that can reduce water supplies for several years at a time and further increase the risk of fish imperilment. On average, drought conditions have occurred in the Southeast every 5 to 10 years since 1895 (NDMC 2004), and localized droughts may occur more frequently (e.g., 2 to 3 years in Georgia; Baker 2000). Droughts cause extremely low streamflows and, in some instances, complete desiccation of lower order streams, resulting in the emigration or local mortality of stream fish assemblages (Bayley and Osborne 1993). Further, increased demand placed on water resources by a growing human population probably will amplify the negative effects of drought on streamflows. Thus, southeastern fishes could suffer significant effects if water management plans do not consider the affects of frequent, natural droughts.

Recently, the Southeast experienced five years of severe drought conditions (USGS 2003). The effects of this drought were evident in the lower Flint River Basin (FRB) located in southwestern Georgia. Groundwater withdrawals for extensive row-crop agricultural irrigation, industrial use, and municipal supply in the lower FRB have averaged approximately 66 million gallons per day over the past 30 years with seasonal peaks in demand occurring in June and July (Mosner 2002). Although normal annual precipitation is usually able to recharge groundwater levels, precipitation reductions during the drought limited recharge, and groundwater levels fell to record lows in response to pumping (Mosner 2002). Streamflows throughout the basin also fell below previously recorded all-time lows in larger streams and completely ceased in several small perennial streams. As a result, local conditions ranged from completely dry streambeds to reaches containing long, disconnected, stagnant pools (Johnson et al. 2001; Mosner 2002; USGS 2003). These severe streamflow reductions caused widespread mortalities of freshwater mussels (Johnson 2001). However, the effects of the severe, prolonged drought on the fish assemblages in the lower FRB and their ability to recover are currently unknown. Therefore, the objectives of this study were to evaluate (1) the effects of drought on the fish assemblages and habitats of the lower FRB and (2) the ability of fish assemblages in the lower FRB to recover from drought conditions. The results from this study eventually will be used to develop streamflow models, which will assist decision makers in protecting the aquatic resources in the lower FRB during future droughts.

CHAPTER 2

LITERATURE REVIEW

Drought is a naturally occurring disturbance that results from an extended period of below-average precipitation (Wilhite 2000). However, the exact nature of drought (i.e., the amount and duration of rainfall deficit) is difficult to define because the conditions that determine drought are dependent upon the climate of a specific region (Humphries and Baldwin 2003; Lake 2000). Thus, definitions of drought must be regionally and temporally specific (Wilhite 2000; Humphries and Baldwin 2003).

Drought definitions can be placed into 4 distinct groups: meteorological, agricultural, hydrological, and economic (WMO 1997; Lake 2000; Wilhite 2000). Meteorological drought occurs when precipitation is below expected levels for a given location over a certain time interval, generally months or years (Palmer 1965). Agricultural drought occurs when the precipitation shortfall results in reduced soil moisture and causes detrimental effects on crop production (Wilhite 2000). Hydrological drought occurs when extended precipitation shortfalls reduce surface water and groundwater supplies, which causes low streamflow, reduced reservoir levels, and wetland drying (Wilhite 2000). Finally, economic drought is the result of the combined effects of meteorological, agricultural, and hydrological drought on the human population and is measured in losses of agriculture-based revenue or widespread famine (Wilhite 2000). Because hydrological aspects of drought (e.g., reduced streamflow) are most important to stream fish, drought is defined here as an “unpredictable low-flow period, which is unusual in its duration, extent, severity, or intensity” following Humphries and Baldwin (2003).

Streams are formed by a combination of multiple water sources. Groundwater inputs maintain baseflow, and rainfall events augment streamflow by producing direct precipitation on the stream channel, overland flow, and shallow, sub-surface flow from the surrounding catchment (Dunne and Leopold 1978). During drought, however, precipitation-derived streamflow generation is greatly decreased, and streamflows primarily derive from groundwater inputs (Changnon 1987; Grigg 1996; Dahm et al. 2003). Groundwater tables can drop below stream levels as drought conditions persist. Streams then become losing reaches where water in the streambed percolates through the substrate and recharges the underlying aquifer (Dahm et al. 2003). As streams continue to lose water to groundwater recharge, streamflow can cease, and streams become fragmented into isolated pools that eventually become completely dry unless a rainfall event occurs (Matthews 1998).

Reduced streamflows during a drought affect fish habitat. Stream width and depth are reduced when streamflows are low, and stream size and habitat availability reductions can result (Resh 1992; Matthews 1998). Relatively shallow, fast-flowing habitats, such as riffles and runs, decrease in size and may even disappear during drought (Boulton and Lake 1990; Matthews 1998; Magoulick and Kobza 2003). Thus, the habitat composition of drought-affected streams tends to be dominated by slow-water habitats such as pools (Larimore et al. 1959; Tramer 1977; Lake 2003).

Drought also affects water temperatures and dissolved oxygen concentrations. More energy is available to heat the water during a drought because air temperature and solar radiation tend to be higher than average. The smaller volume of slow or stagnant water that occurs during low streamflow also is heated more rapidly (Matthews 1998). Consequently, water temperatures usually increase during a drought and may reach lethal levels during summer when air temperatures are highest (Matthews 1998). An increase in water temperature can result in a simultaneous decrease in dissolved oxygen concentration because oxygen solubility decreases with increases in water temperature (Horne and Goldman 1994), and stagnant pools are poorly aerated. Thus, dissolved oxygen concentrations can fall to hypoxic or anoxic levels when temperatures are high and natural aeration is limited during a drought (Matthews 1998; Lake 2003).

Changes in habitat during drought can negatively affect stream fish. Fish become crowded into smaller habitats and are found at higher densities when stream size shrinks (Larimore et al. 1959; Tramer 1977; Matthews 1998; Labbe and Fausch 2000). At high densities, predation rates can increase because predators have easier access to prey (Matthews 1998). Further, drought can cause reductions in macroinvertebrate populations (Larimore et al. 1959; Canton et al. 1984; Cowx et al. 1984), which result in declines of important food sources for stream fish. Stream fish also may succumb to low dissolved oxygen concentrations and high temperatures that occur during drought (Larimore et al. 1959; Tramer 1977; Hess et al. 1999).

Drought also may reduce stream fish populations and change fish assemblage structure. Drought can reduce egg, larval, and juvenile survival, which can result in year class failure of some stream fishes (Cowx et al. 1984; Davies et al. 1988). Reductions in species richness also have been documented in drought-affected streams (Larimore et al. 1959; Tramer 1977). Further, hypoxic conditions can restructure warmwater stream fish assemblages by favoring hypoxia-tolerant species and reducing intolerant species (Smale and Rabeni 1995). Thus, stream fish assemblages during a drought are likely to be dominated by adult fish that are tolerant of high temperatures and low dissolved oxygen concentrations.

Although severe drought often has negative effects, aquatic biota have developed physiological and behavioral adaptations for coping with drought conditions. Some fish species, such as bowfin (*Amia calva*) are capable of gulping air during hypoxic periods and may undergo aestivation in moist substrates if they become stranded when streamflow recedes (Jenkins and Burkhead 1993). Aquatic macroinvertebrates may seek refuge in oxygenated water of the hyporheic zone when streams dry during drought (Williams and Hynes 1974; Canton et al. 1984). Additionally, some darter species (*Etheostoma* sp.) also may be able to survive in the hyporheic zone (Tramer 1977). Before streams completely dry, however, fish in some regions may move to refugia such as pools that still contain water (Larimore et al. 1959; Gelwick 1990) or larger downstream reaches (Detenbeck et al. 1992; Magoulick and Kobza 2003). In contrast, Bayley and Osborne (1993) inferred that downstream fish movement in Illinois streams did not occur when small streams dried during a drought because they found no increases in species richness or biomass in permanently flowing, downstream reaches. Thus, downstream movement in response to drought may be specific to regions or river basins.

Most stream fish communities are resilient and can recover quickly after a disturbance. Fishes tend to move back into an affected area as soon as the disturbance has subsided (Larimore et al. 1959; Peterson and Bayley 1993), and fish assemblages can return to pre-disturbance levels within one year (Larimore et al. 1959; Meffe and Sheldon 1990; Bayley and Osborne 1993). In relatively small-sized disturbances, “haphazard” fish movement may be sufficient for recolonizing affected areas (Peterson and Bayley 1993), but large-scale seasonal upstream migrations of adult fish are required for recolonization of extensive areas (Larimore et al. 1959;

Bayley and Osborne 1993). Thus, seasonal fish movement likely is the mechanism by which stream fishes recolonize drought-affected streams.

Presently, there is little information describing the effects of drought and recovery of fish assemblages in southeastern coastal plain streams. Coastal plain streams in the Southeast typically are low gradient and contain relatively few riffles. Therefore, the drying process during drought may be different in these streams than in temperate, higher-gradient streams. Further, the southeastern climate generally experiences less seasonal variation than temperate regions. Winter in the Southeast is relatively short and mild, and summer conditions are longer than most temperate climates. Thus, temperature-related effects of drought on habitat may occur for longer periods in southeastern coastal plain streams than in northern, temperate streams. Relatively little also is known about seasonal habitat requirements and movement patterns of coastal plain fishes. This study of lower FRB fish assemblages will provide information about drought effects on warmwater coastal plain stream fish assemblages and their ability to recover.

CHAPTER 3

METHODS

Study Area and Design

I examined the influence of drought on fish assemblages in the lower FRB. The lower FRB is a network of relatively low-gradient, warmwater streams located below the fall line in southwestern Georgia. The lower FRB lies predominantly within the Fall Line Hills and Dougherty Plain districts of the Coastal Plain physiographic province (Figure 1; Clark and Zisa 1976). Streams flowing through the undifferentiated residuum geologic layer of the Fall Line Hills district are characterized by sandy-mud substrate and relatively high turbidity levels, whereas streams in the Dougherty Plain district often dissect carbonate rocks of the Ocala Limestone formation and are characterized by coarse substrates and low turbidity. Most streams in the Fall Line Hills district are dominated by surface water inputs, while streams in the Dougherty Plain generally receive substantial amounts of groundwater from the underlying Floridan Aquifer (Hicks et al. 1987; Johnson 2001; Mosner 2002).

I sampled stream fish assemblages and habitats at 19 sites on 11 tributaries in the lower FRB (Figure 2). Sample sites were located on streams of various groundwater influence and size with 10 sites in the Fall Line Hills district and nine sites in the Dougherty Plain district (Table 1). Groundwater is important to warmwater stream fishes because groundwater influenced areas can provide thermal refugia during periods of temperature-related stress (Gorman and Karr 1978; Schlosser 1982; Peterson and Rabeni 1996). In the lower FRB, conductivity levels are directly related to groundwater inputs in streams (R. Jackson, University of Georgia; personal communication). Thus, I classified eight sites in the Dougherty Plain district and four sites in the Fall Line Hills district as groundwater influenced (mean conductivity > 100 µS/cm). I classified the seven remaining sites as surface water dominated (mean conductivity < 100 µS/cm). Stream size also is important to consider in an assemblage level study because fish assemblage structure is often related to stream size (Osborne and Wiley 1992). I used link magnitude to describe stream size for each study site because stream order (Strahler 1957) does not accurately describe stream size in the lower FRB (R. Jackson, University of Georgia; personal communication). Link magnitude is defined as the number of first order stream segments upstream of a given stream reach (Osborne and Wiley 1992). The link magnitude ranged from 2 to 807 for the sample sites in this study.

Sampling was conducted during the drought years of 2001 and 2002 and during the non-drought year of 2003. During all seasons of the drought, streamflows were well below average Additionally, streamflows during the drought summers reached record lows in some streams. During the non-drought year, however, streamflows were average or above. Because of the reduced streamflows, mean stream width, depth, and current velocity, were lower during the drought years than during the non-drought year (Table 2).

Because stream fish assemblage structure can vary seasonally (Vadas 1991; Vadas 1992; Peterson and Rabeni 1996), each sample site was sampled once during winter, spring, and summer of each year to evaluate temporal variation in fish assemblage structure and drought effects in the lower FRB. Winter sampling was conducted during January - March, spring sampling during April - June, and summer sampling during July - September. Two summer 2003 samples were conducted on October 1st and 2nd because of high streamflow.

In all samples, site length was sufficient to include all representative habitat types and minimize the effect of localized species-specific distribution patterns (Peterson and Rabeni 1995). During summer 2001, winter 2002, and spring 2002, length of wadeable sites (mean depth < 1 m) averaged 54.5 m (range 35 – 75 m), and length of non-wadeable sites averaged 100.1 m (range 90 – 110 m). Although these lengths included all available habitats, I concluded that increasing site length and sampling several replicates of available habitats at a site would result in more precise fish and habitat samples. Thus, during summer 2002, winter, spring, and summer 2003, I sampled, on average, 50 additional meters at each site resulting in a mean length of 98.6 m (range 77 – 129 m) in wadeable sites and 152.7 m (range 145 – 165 m) in non-wadeable sites.

The lowest consecutive 7-day streamflow likely to occur in a 10-year period (7Q10) often is used as a benchmark for identifying and evaluating drought conditions. To estimate the severity of drought conditions at each sample site during sampling, I used the USGS stream gauging station (number 02353500) at Ichawaynochaway Creek in Milford, Georgia to determine if streamflows were below monthly 7Q10. I chose this gauging station because continuous streamflow data were available for the duration of this study, monthly 7Q10 levels previously had been determined, and streamflow at that site was highly correlated with streamflow at the sample sites (mean Pearson $r = 0.77$). I determined a sample site to be below monthly 7Q10 if the streamflow at the gauging station was below 7Q10 on the date of the sample.

Fish Sampling

Electrofishing is a sampling method that is influenced by biological, environmental, and technical factors (Reynolds 1996). Vulnerability to electrofishing varies among species and size classes because of differences in morphology, physiology, and behavior. Environmental conditions such as water conductivity, temperature, turbidity, and physical habitat structure also affect electrofishing efficiency. Further, electrofishing gears differ in efficiency and application. Because I examined fish assemblages in streams of various sizes and habitats, I used the most efficient electrofishing method for each site. I also followed sampling protocols that allowed me to adjust catch data with gear-specific sampling efficiency models (Bayley and Dowling 1990). I conducted all fish sampling during daylight hours from 1/2 hour after sunrise to 1/2 hour before sunset.

In narrow, wadeable streams (mean wetted width < 10 m, mean depth < 1 m), the upstream and downstream boundaries of a site were blocked off with 7-mm mesh nets and sampling was conducted with a Smith-Root LR 24 pulsed DC backpack electrofisher operating at approximately 0.25 A pulsed DC. Stunned fishes were collected by a 3-person sampling crew during three passes. The first pass was made in an upstream direction, followed by a downstream pass, and a final upstream pass. The electrofisher was carried by one crewmember while stunned fish were retrieved by two additional crewmembers. Fish that drifted into the downstream blocknet during sampling were removed and included in the sample. The blocknets were removed following sampling and fish were identified and measured.

In wide (mean wetted width > 10 m), wadeable streams, the upstream and downstream boundaries of the site were blocked off with 7-mm mesh nets and sampling was conducted with a tote-barge-mounted Smith-Root Type VI-A electrofishing unit powered by a 3,000 watt three-phase generator. Sufficient voltage was used to maintain approximately 3 A pulsed DC. The same three-pass protocol described for backpack electrofishing was followed. The tote-barge was maneuvered by one crewmember, while stunned fish were collected by the other two crewmembers who carried anode poles that were attached to the electrofishing unit by 7.62 m cables. The cable length allowed each crewmember to cover over half of the stream width as they walked in a zigzag pattern from one bank to the center of the stream during each pass. A fourth crewmember ferried captured fish to an aerated holding tank on the tote-barge. Fish that drifted into the downstream blocknet during sampling were removed and included in the sample. The blocknets were removed following electrofishing, and the fish were identified and measured.

In deep (mean depth > 1 m), non-wadeable sites, sampling was conducted with a Smith-Root Type VI-A electrofishing unit that was mounted on a 4.3 m johnboat equipped with two Wisconsin rings. The unit was powered by a 3,000 watt three-phase generator operating at approximately 3 A pulsed DC. Blocknets were not required for boat electrofishing samples because the gear efficiency models were parameterized without their use (Peterson 1996). Sampling consisted of six passes; the first pass was made in an upstream direction in the middle of the stream; the second was in a downstream direction adjacent to the first, but along one of the banks; and the third pass was made in an upstream direction along the opposite bank. The next three passes were identical to the first three with the direction (upstream or downstream) reversed. Fish were held in an aerated tank until all passes were complete.

All fish were identified to species and total length (TL) was measured to the nearest millimeter (mm). Large fish (>100 mm) and all Centrarchidae and Catastomidae were identified, measured, and released; small fish (<100 mm) were preserved in 10% formalin and taken to the laboratory for identification and more accurate measurement. Fish were weighed to the nearest gram to determine length-weight relationships. The lengths and weights of preserved fish were corrected for shrinkage and weight loss with the correction factors developed by Ruiz and Peterson (2002).

Physical Habitat Measurements

I used a line-transect method to measure physical habitat characteristics at each sample site after fish sampling and block net removal (Arend and Bain 1999). Using summer 2001 habitat data as a preliminary study, I determined that the optimal habitat sampling protocol was to measure habitat characteristics at eight points along 10 evenly-spaced transects (Figure 3; McCargo and Peterson 2002). At each transect, I measured wetted stream width (to the nearest 0.1 m) perpendicular to flow. I visually estimated mesohabitat and substrate composition in a 1-m wide band centered along each transect. I classified mesohabitats as side channel, edgewater, pool, run, riffle, or race following Arend (1999). I classified substrate as silt (<0.5 mm), sand (0.5-2 mm), gravel (2-20 mm), cobble (20-200 mm), boulder (>200 mm), and bedrock (no particles). At each point along a transect, I measured mean current velocity (to the nearest 0.01 m/s) with a Marsh-McBirnney digital flow meter and depth (to the nearest 0.01 m) with a standard top-set wading rod. When water depth was less than 0.65 m, I measured average velocity at 0.6 of total depth; at greater depths, I measured average velocity as the mean of readings taken at 0.2 and 0.8 of total depth. For each site, I estimated mean current velocity and mean water depth by averaging each point measurement, and mean wetted width by averaging the widths of each transect. Further, I calculated mean mesohabitat composition by summing the percentages of each mesohabitat type and dividing by the number of transects. Because sites differed in length, I calculated standardized mesohabitat area for 100 m of stream length by multiplying average mesohabitat percentages by mean wetted width and 100 m.

I also estimated large wood density at each sample site. I defined large wood as pieces greater than 10 cm in diameter and at least 1 m long that were lying in the wetted stream channel. Rootwads or groups of smaller pieces of wood were counted as 1 piece. In summer 2001, I measured large wood density by estimating percent wetted surface area covered by large wood; however, preliminary analysis indicated that this method was inaccurate. For the remaining samples, I calculated large wood density by dividing the total number of large wood pieces by wetted surface area. I used linear regression to estimate large wood density from summer 2001 percent wetted surface area coverage estimates. I used summer 2001 percent large wood as the predictor variable and winter 2002 large wood density estimates as the response variable. I then used the resulting linear equation to predict summer 2001 large wood density for each site. I also measured conductivity, turbidity, water temperature, and dissolved oxygen prior to sampling at each site using calibrated, hand held meters.

Definitions and Statistical Analyses

Species assemblage metrics are used to describe the state of an aquatic ecosystem by examining the composition and relative abundance of species (Kwak and Peterson *in press*). Species richness is defined as the total number of species found in a given area (McIntosh 1967; Krebs 1999). High species richness values often indicate a high quality system, whereas low values can indicate a poor quality system or environmental degradation. I calculated adjusted species richness estimates for each sample using gear-specific models developed for each sampling protocol (Bayley and Dowling 1990).

Diversity indices are used to examine the commonness and rarity of species in an assemblage by combining information on species richness and their relative abundance (Morin 1999; Kwak and Peterson *in press*). Assemblages with high fish species diversity contain many species with approximately equal abundances, whereas low fish species diversity generally indicates few species or assemblages dominated by a relatively small number of species. To describe fish species diversity at each sample site, I calculated Shannon-Weaver's Diversity index (*H'*) using the equation

$$H' = \sum_{i=1}^{s} (p_i)(\log_e p_i)$$

where s is the number of collected species, and

p_i is the proportion of the total sample represented by the *i*th species (Shannon and Weaver 1949).

I used sampling efficiency-adjusted abundance estimates when calculating the proportion of individuals for each species.

Total assemblage biomass is commonly used as an indicator of stream productivity (Ney 1999) and also can be used to determine stream fish assemblage habitat use patterns (Peterson and Rabeni 1996; Peterson and Rabeni 2001). Productive streams or habitats can support large amounts of biomass, and non-productive streams or habitats support small amounts of biomass. I calculated total assemblage biomass (g/m^2) by applying species-specific length-weight regressions to adjusted length-frequency data, summing each species' mass, and dividing the resulting total fish mass by site wetted surface area. For ease of interpretation, I converted biomass from g/m^2 to kg/ha.

Biotic indices use the presence, absence, and relative abundance of tolerant and intolerant species to assess the health of an aquatic ecosystem (Ney 1999). The Index of Biotic Integrity

(IBI) uses metrics based on fish species composition, trophic composition, abundance, and condition to assess the biological integrity of streams (Karr 1981; Kwak and Peterson *in press*). Low IBI scores indicate stream degradation, and high scores indicate an overall 'healthy' stream. I calculated IBI scores by using adjusted length-frequency data and the metrics developed for the FRB by the Georgia Department of Natural Resources (Schleiger 2000). For ease of interpretation, I also grouped IBI scores into the following descriptive categories: very poor $\leq$ 18; poor 19 – 26; fair 27 – 33; good 34 – 41; very good $\geq$ 42 following Karr (1981).

Habitat diversity is a metric used to describe stream habitat complexity and often is positively related to fish species diversity (Gorman and Karr 1978; Schlosser 1982). To examine this relationship in the lower FRB, I measured stream habitat diversity in two dimensions (i.e., stream depth and current velocity) following Gorman and Karr (1978). I grouped depth and velocity measurements made at each point along a transect into six categories based on quantiles for the entire data set (Table 3). I treated each unique combination of depth and velocity group (e.g. velocity group 1 x depth group 3) as a species, and calculated stream habitat diversity with Shannon-Weaver's index (described above).

Matched pairs *t*-tests are used to test for differences between two groups when observations in one group are correlated with observations in another (Zar 1996). In this project, samples collected at each site during each drought and non-drought season can be considered matched pairs. Thus, I used matched pairs *t*-tests to examine differences in fish assemblages and habitat availability between drought and non-drought years. I tested for differences in fish assemblages by comparing species richness, fish species diversity, biomass, and IBI for each season. I tested for differences in habitat availability by comparing standardized mesohabitat area for each season. I also tested for differences in turbidity, water temperature, and dissolved oxygen for each season. Positive differences indicated higher values for non-drought conditions, and negative differences indicated higher values during drought conditions. For all *t*-tests, I considered differences significant at a 0.10 alpha level and constructed 90% confidence intervals to examine precision. Prior to analysis, I conducted a Shapiro-Wilk's test and examined a normal probability plot to determine if the fish assemblage data met normality and equal variance assumptions. If the data were non-normal or heteroscedastic, then the response variables were transformed, rechecked for normality, and the *t*-tests were re-run.

Multiple linear regression is a widely used statistical technique that simultaneously assesses the influence of several predictor variables on a response (Neter et al. 1996). This technique, however, is not applicable when samples are dependent (Sokal and Rohlf 1995). In this study, samples were dependent because I collected multiple samples at the same sites. To account for the dependence, I used hierarchical linear models to examine the effects of stream site characteristics on fish assemblage response variables (i.e., species richness, fish species diversity, and biomass) for each season. Hierarchical linear models account for dependence among sites by including random effects that represent unique, site-specific effects on an assemblage (Sniders and Bosker 1999).

I used an information-theoretic approach (Burnham and Anderson 1998) to evaluate the fit of the hierarchical linear regression models relating sample site characteristics to fish assemblage metrics. For each response and season, I constructed a global model consisting of main and two-way interaction effects as predictors that I hypothesized to influence fish assemblages in the lower FRB (Table 4). Multi-way interactions (i.e., three-way, four-way, etc.) were not included in the global model because the number of samples was insufficient. I then constructed ecologically meaningful candidate models that were subsets of the global model. I included stream link magnitude in all candidate models because fish assemblages are known to vary with stream size (Osborne and Wiley 1992). Sample site area was greater during the non-drought year because of increased stream width and because I sampled longer stream reaches during summer 2002 and all seasons of 2003. Thus, I included sample site area in the species richness and fish species diversity models to determine if fish assemblages were more influenced by sample site area or by other stream site characteristics (e.g., drought). I assessed goodness-of-fit via residual analysis for the global model for each response variable and season. If the residuals indicated non-normality or heteroscedasticity for any season, the response variable was natural log-transformed, rechecked for normality, and then the models were re-fit.

I used Akaike's Information Criteria (AIC; Akaike 1973) with the small sample bias adjustment (AIC_c; Hurvich and Tsai 1989) to evaluate the fit of each candidate model based on Akaike model weight. Akaike model weights range from zero to one and are interpreted as the probability that the model with the highest weight is the best fitting model relative to the other candidate models (Burnham and Anderson 1998). I constructed a confidence set of models that contained models with Akaike weights that were within 10% of the best fitting model weight. A confidence set of models is analogous to the confidence interval of a mean and is used so that inferences are based on several plausible models rather than just one. The 10% cutoff point is similar to 12.5% suggested by Royall (1997) as a basis for evaluating strength of evidence.

Model averaging is used to incorporate model selection uncertainty into parameter estimates. However, this technique is not appropriate for hierarchical linear models that contain fixed and random effects (K. Burnham, Colorado State University; personal communication). Therefore, instead of basing inferences and predictions on a single best model, I calculated the estimates of fixed and random effects for the models in the confidence set. When the confidence set contained more than five models, I calculated parameter estimates for a subset of the best fitting models to simplify analysis. I developed the subset of models, hereafter referred to as the inference set, by examining the importance weights for each predictor variable and the Akaike weights for each model. Importance weights are used to compare the strength of the relationship among predictor variables (Burnham and Anderson 1998) and are calculated by summing the Akaike weights for each model that contains the variable of interest. Models that only contained variables with relatively high importance weights and that were among the best fitting models (i.e., had high Akaike weights) were included in the inference set. For ease of interpretation, I also limited the inference set to the six best fitting models. I calculated the parameter estimates for each model with the GLIMMIX macro in Statistical Analysis Software (SAS) version 8.02 (SAS Institute 2001) and evaluated the precision of each fixed and random effect by computing 90% confidence intervals based on a *t*-statistic with *n*-1 degrees of freedom (Littell et al. 1996).

Chi-square tests are used to compare frequencies of occurrence between two or more groups (Zar 1996). I used chi-square tests to determine which fish species were most affected by drought by comparing the frequency of occurrence of each species sampled during drought and non-drought years. The null hypotheses for these tests were that each species would occur with the same frequency among samples during drought and non-drought years. For example, if a particular species were collected in 13 of the 38 (34%) summer drought samples and 6 of the 17 (35%) summer non-drought samples then the null hypothesis would not be rejected. I considered frequencies of occurrence significantly different at the alpha = 0.10 level. I also calculated odds ratios to determine the magnitude of difference in frequencies of occurrence between drought and non-drought summers. Odds ratios are non-negative numbers that describe the likelihood of a success (i.e., presence of a species in summer drought samples; Agresti 2002).

CHAPTER 4

RESULTS

I collected drought samples at all 19 sites during summer 2001, summer 2002, and spring 2002. I was unable to sample one site (MUC2) during winter 2002 because of high streamflow. Similarly, I only was able to collect non-drought samples at 11 sites during winter 2003 and at 17 sites during spring and summer 2003 because of persistent, high streamflows. Additionally, habitat sampling was incomplete for 11 samples. I was unable to measure current velocity during 6 sample occasions because of equipment failure. To estimate mean velocity for these samples, I estimated discharge by using the most strongly correlated USGS stream gauging station (Appendix A) and divided the discharge estimate by the mean cross sectional area (product of mean depth and mean stream width). I collected fewer than 10 habitat transect measurements (range 4 - 8) on six sample occasions because of inclement weather. For these samples, I used the limited transect data to calculate mean habitat values.

Streamflow at each site varied considerably within and among years and was well below average because of prevailing drought conditions during 2001 and 2002. During the drought years, streamflows were, on average, lowest in spring and highest in winter. I estimated that 61% of the sites were at or below monthly 7Q10 during winter 2002 sampling, 100% of the sites were at or below monthly 7Q10 during spring 2002 sampling, and 79% and 47% of the sites were at or below monthly 7Q10 during summer 2001 and 2002 sampling, respectively (Table 5). Drought conditions subsided during fall 2002, and streamflows returned to normal or above in

2003. During the non-drought year, streamflows were, on average, lowest in summer and highest in spring. I estimated that only 1 site (KIN3) was at or below monthly 7Q10 during winter 2003 sampling, and no sites were at or below monthly 7Q10 during spring and summer 2003 sampling (Table 5).

I collected a total of 21,470 fish in 122 samples during my study. These fishes consisted of 60 species representing 17 families (Appendix B). Most (48%) fish were collected during the summer months and the fewest (24%) during the winter (Table 6). Gear-efficiency-adjusted fish abundance was much greater during all seasons of the non-drought year than during all seasons of the drought years because sampling efficiency was lower during the non-drought year than during the drought years (Table 6). Further, similar numbers of species were captured during drought and non-drought years (Table 6), but adjusted species richness was higher, on average, during the non-drought year than during the drought years, especially in small streams (link magnitude < 300; Figure 4).

Overall Drought Effects on Fish Assemblages

The Shapiro-Wilk's test ($W = 0.952$, $P < 0.001$) and the normal probability plot indicated non-normal species richness data. Thus, matched pairs *t*-tests were performed with natural log-transformed species richness values. Matched pairs *t*-tests indicated statistically significant differences in species richness between drought and non-drought years during spring ($t = 2.851$, 16 df, $P = 0.01$) and summer ($t = 3.741$, 33 df, $P < 0.01$) but not winter ($t = 1.366$, 10 df, $P = 0.20$). Species richness was significantly higher during the non-drought year spring and summer (Figure 5a).

There were not significant differences in fish species diversity between drought and non-drought years during winter (*t* = -0.692, 10 df, *P* = 0.51) and spring (*t* = 1.349, 16 df, *P* = 0.20), but there was a significant difference in diversity between drought and non-drought years during summer (*t* = 1.805, 33 df, *P* = 0.08). Diversity was significantly higher in the non-drought summer than in the drought summers (Figure 5b).

The Shapiro-Wilk's test (W = 0.720, *P* < 0.001) and the normal probability plot indicated non-normal biomass data. Thus, matched pairs *t*-tests were performed with natural log-transformed biomass values. Biomass was significantly different between drought and non-drought years in winter (*t* = -2.157, 10 df, *P* = 0.06) and summer (*t* = 2.112, 33 df, *P* = 0.04) but not in spring (*t* = 1.042, 16 df, *P* = 0.31). On average, biomass was significantly lower in the non-drought year during winter and significantly higher in the non-drought year during summer (Figure 6a).

IBI was significantly different between drought and non-drought years in spring (*t* = 3.588, 16 df, *P* < 0.01) and summer (*t* = 3.995, 33 df, *P* < 0.01), but not winter (*t* = 1.336, 10 df, *P* = 0.21). IBI was significantly higher in the non-drought year during spring and summer (Figure 6b). The significantly higher IBI during non-drought years resulted in the classification of more sites as 'good' rather than 'fair'. During the drought spring, 9 sites (47%) were classified as 'fair', and 10 sites (53%) were classified as 'good', whereas 1 site (6%) was classified as 'fair', and 16 sites (94%) were classified as 'good' during the non-drought spring. During the drought summers, 18 sites (47%) were classified as 'fair', and 20 sites (53%) were classified as 'good', but in the non-drought summer, 2 sites (12%) were classified as 'fair', and 15 sites (88%) were classified as 'good'.

Overall Drought Effects on Habitat

Matched pairs *t*-tests indicated statistically significant differences in mesohabitat area between drought and non-drought years for all seasons (Table 7). Significantly more run habitat was available during all seasons of the non-drought year (Figure 7). Significantly less pool habitat was available during the non-drought winter and spring, but there was no significant difference in pool habitat area between drought and non-drought summers. Riffle habitat was only observed during the drought years. Thus, less riffle habitat was available during all seasons of the non-drought year, but the difference was significant only in summer because of small sample sizes in winter and spring (Table 7). During the non-drought summer, sample sites contained significantly less side channel and more edgewater and race habitat. During winter and spring, however, there were no significant differences in edgewater, side channel, and race habitat area.

Matched pairs t-tests also indicated statistically significant differences in physicochemical parameters between drought and non-drought years in all seasons (Table 8). Dissolved oxygen concentrations were significantly higher during the non-drought year in winter and spring, but there were no significant differences in dissolved oxygen concentrations during summer. There also were no significant differences in turbidity between drought and non-drought year winters. However, turbidity was significantly higher during the non-drought year in spring and summer. Water temperatures, on average, were significantly higher during the drought year in winter and summer, but there were no detectible differences in water temperature during spring.

Modeling Large Scale Effects on Fish Assemblages

Residual analysis for the global model predicting species richness indicated non-normal, heteroscedastic data. Thus, I used natural log-transformed species richness values in the hierarchical linear modeling procedure for all seasons. The best fitting model predicting species richness during winter contained link, groundwater, link*groundwater interaction, and sample site area (Appendix C1). Parameter estimates for the best fitting model indicate that species richness was positively related to link magnitude and groundwater (Table 9). However, the negative link*groundwater interaction indicates that the groundwater effect varied with stream size. Species richness increased as stream size increased, was higher in small groundwater influenced streams than in small surface water dominated streams, but was similar in large groundwater influenced and large surface water dominated streams (Figure 8). Further, the positive relationship between sample site area and species richness indicates that species richness increased with increases in sample site area. While strongest evidence is indicated for the effects in the best fitting model, some evidence also is indicated for drought effects (Table 10). The negative relationship between species richness and drought indicated by parameter estimation suggests that species richness was higher during the non-drought winter than during the drought winter (Figure 9).

The best fitting model for species richness during spring contained link and drought (Appendix C3). The importance weights indicate strongest evidence for the drought effect (Table 10), and parameter estimates for the best fitting model indicate that species richness was positively related to link magnitude and negatively related to drought (Table 9). In general, species richness increased as stream size increased and was higher during the non-drought year than during the drought year (Figure 10). Although importance weights provide some evidence for groundwater, sample site area, and large wood density effects on species richness during spring, the parameter estimates were imprecise and the exact nature of the effects could not be determined (Appendix C4).

The best fitting model for species richness during summer also contained link and drought (Appendix C5), and the importance weights indicate strongest evidence for the drought effect (Table 10). Parameter estimates for the best fitting model indicate that species richness was positively related to link magnitude and negatively related to drought (Table 9). Species richness increased as stream size increased during both drought and non-drought years and was higher during the non-drought year than during the drought year (Figure 11). Although not included in the best fitting model, some evidence for the link*groundwater interaction is indicated by its importance weight (Table 10). Species richness does appear to be similar during drought and non-drought years in large streams (Figure 11). Thus, the drought likely had a larger effect in smaller streams during summer.

The best fitting model for fish species diversity during winter contained link, drought, and link*drought interaction (Appendix C7). Parameter estimates for the best fitting model indicate that fish species diversity was negatively related to link magnitude and drought (Table 11). However, the positive link*drought interaction suggests that the stream size effect on fish species diversity varied between drought and non-drought years. During the drought year, fish species diversity increased as stream size increased, but during the non-drought year fish species diversity decreased as stream size increased such that fish species diversity was higher in small streams (link magnitude < 300) during the non-drought year but lower in large streams during the non-drought year (Figure 12). Although some evidence is indicated for sample site area and groundwater effects (Table 12), the precise nature of these effects could not be determined because the confidence intervals of their parameter estimates were wide and contained zero (Appendix C8).

The best fitting model for fish species diversity during spring contained link, habitat diversity, link*habitat diversity interaction, and sample site area (Appendix C9). Parameter estimates for the best fitting model indicate that fish species diversity was positively related to link magnitude and habitat diversity (Table 11). However, the negative link*habitat diversity interaction indicates that the stream size effect varied with habitat diversity. In sites with low habitat diversity, fish species diversity increased as stream size increased, whereas fish species diversity in sites with high habitat diversity did not change with stream size (Figure 13). Additionally, fish species diversity was lower in small streams with low habitat diversity than in small streams with high habitat diversity, but fish species diversity was similar in large streams with low and high habitat diversity. Because fish species diversity was negatively related to sample site area in the best fitting model (Table 11), fish species diversity decreased as sample site area increased.

The best fitting model for fish species diversity during summer contained link, habitat diversity, and large wood density (Appendix C11). Parameter estimates for the best fitting model indicate that fish species diversity was positively related to habitat diversity and negatively related to large wood density (Table 11). On average, fish species diversity was higher in areas of high habitat diversity and decreased as large wood density increased (Figure 14). Link magnitude was slightly positively related to fish species diversity, but the 90% confidence interval for the parameter estimate in the best fitting model contained zero so the precise nature of the stream size effect could not determined (Table 11).

Residual analysis for the global model predicting biomass indicated non-normal, heteroscedastic data. Thus, I used natural log-transformed biomass values in the hierarchical linear modeling procedure for all seasons. The best fitting model for biomass during winter contained link, groundwater, habitat diversity, and groundwater*habitat diversity interaction (Appendix C13). Biomass was negatively related to groundwater and habitat diversity in the best fitting model, but the positive groundwater*habitat diversity interaction indicates that the habitat diversity effect varied with groundwater (Table 13). Biomass increased as habitat diversity increased in groundwater influenced streams, but biomass decreased as habitat diversity increased in surface water dominated streams (Figure 15). Although drought and link*groundwater interaction were not included in the best fitting model, their importance weights offer some evidence for their effects on biomass during winter (Table 14). Biomass was positively related to drought in additional models of the candidate set, and the negative link*groundwater interaction indicates that the stream size effect varied with groundwater influence (Appendix C14). Biomass increased with stream size in surface water dominated streams, decreased with stream size in groundwater influenced streams, and was higher in small groundwater influenced streams than in small surface water dominated streams (Figure 16). Models also predicted that biomass was higher during the drought year winter than during the non-drought year winter (Figure 16).

The best fitting model for biomass during spring contained link alone (Appendix C15). Parameter estimates for the best fitting model indicate a very weak relationship between biomass and link magnitude (Table 13). However, importance weights indicate relatively strong evidence for groundwater and drought effects and additional evidence for groundwater*drought interaction and link*groundwater interaction effects (Table 14). In the additional models, the positive relationship between biomass and groundwater (Appendix C16) indicates that groundwater influenced streams contained more biomass than surface water dominated streams. However, the negative drought*groundwater interaction indicates that the groundwater effect varied with drought conditions. Biomass was higher in groundwater influenced streams than in surface water dominated streams during the non-drought year, but biomass was similar in groundwater influenced streams and surface water dominated streams during the drought year (Figure 17). The precise nature of the link*groundwater interaction effect could not be determined because the confidence intervals for the were wide and contained zero.

The best fitting model for biomass during summer contained link, groundwater, and link*groundwater interaction (Appendix C17). The best fitting model predicts that biomass was positively related to link and groundwater, but the negative link*groundwater interaction indicates that the groundwater effect varied with stream size (Table 13). Biomass was higher in small (link magnitude < 300), groundwater influenced streams than in small, surface water dominated streams, but biomass was slightly higher in large, surface water dominated streams than in large groundwater influenced streams (Figure 20a). Importance weights also indicate evidence for drought and habitat diversity effects (Table 14). Biomass was negatively related to drought in additional models, but the positive link*drought interaction indicated that the drought effect also varied with stream size (Appendix C18). Biomass was higher in small streams during the non-drought year than during the drought year, but in large streams, biomass was lower during the non-drought year than during the drought year (Figure 18b). The precise nature of the habitat diversity effect could not be determined because the 90% confidence interval was very wide and contained zero.

Drought Effects on Species Occurrence

I examined the differences in species occurrence between drought and non-drought years during spring and summer because the matched pairs t-tests and hierarchical linear regression analysis indicated significant drought effects on species richness during both seasons. The chi square analysis indicated significantly different frequencies of occurrence between drought and non-drought years for six species during spring and seven species during summer. During spring, clear chub, a small-bodied species, were 5.19 times more likely to occur in the drought year, while large-bodied fishes such as bowfin, largemouth bass, redear sunfish, redfin pickerel, and warmouth were more likely to occur in the non-drought year (Table 15). During summer, swamp darter were 4.2 times more likely to occur during the drought years, whereas the small-bodied species, redeye chub, and large bodied fishes such as bowfin, greater jumprock, and warmouth were more likely to occur during non-drought conditions.

CHAPTER 5

DISCUSSION

My study was conducted during and in the year following one of the most severe, extended droughts in the recorded history of the lower FRB (Mosner 2002; USGS 2003). During this drought, streamflow in small headwater streams and in portions of larger streams ceased for extended periods of time (Johnson et al. 2001). In 2001 and 2002, approximately 72% of my samples were collected when streamflows were at or below monthly 7Q10, and streamflow was undetectable at several sample sites. Although my sample sites were never completely desiccated, their fish assemblages and habitats were affected by the drought.

The structure of fish assemblages in lower FRB streams differed substantially between drought and non-drought years. On average, there were five fewer species at each site during the drought year spring and summers than during the non-drought year spring and summers. Because seven species also were collected significantly less often during the drought, the response of fishes to reduced streamflow was likely species-specific. I believe that these changes in the stream fish assemblages and species presence probably were caused by factors related to reductions in streamflow during the drought. Stream fish distribution and assemblage structure are largely the result of variation in habitat structure, food availability, and disturbance regime (Schlosser 1987; Peterson and Rabeni 2001). Thus, the process of evaluating the effects of drought on fish assemblages becomes one of understanding the factors influencing fish distribution and assemblage structure in stream systems.

Stream-fish assemblage structure often is related to habitat structure along a longitudinal stream gradient (Gorman and Karr 1978; Vannote et al. 1980; Schlosser 1982; Meffe and Sheldon 1988; Paller 1994). In general, relatively small, upstream reaches contain shallower and less diverse habitats than larger streams (Schlosser 1987; Peterson and Rabeni 2001). Generally, large-bodied fishes are found in deeper habitats presumably because they are more vulnerable to terrestrial predators in shallow habitats (Power 1984). Conversely, small-bodied fishes generally avoid deep habitats because they are vulnerable to aquatic predators but less vulnerable to terrestrial predators (Harvey and Stewart 1991). During the drought, my study sites were, on average, 0.25 m shallower than they were during the non-drought year, which suggests that there were fewer deep-water habitats available, particularly in the smaller streams. Larger-bodied fishes would have been more vulnerable to predation in the smaller, shallower habitats during the drought. Indeed, large-bodied species (e.g., bowfin and largemouth bass) were found significantly less often during the drought year spring and summers. Therefore, I hypothesize that the absence of larger-bodied fishes was due, in part, to the lack of deeper habitats during the drought.

Food availability also influences stream fish assemblage structure. Most small-bodied fish species and juvenile large-bodied species found in the lower FRB feed on macroinvertebrates, and a high proportion of those species are drift feeders that require habitats with relatively high current velocities (Jenkins and Burkhead 1993). Because stream fish often select habitats with higher food abundances (Petty and Grossman 1996), fish assemblage structure presumably is influenced by the availability of higher current velocity habitats and food availability. Previous studies have shown that macroinvertebrate production and abundance are reduced during droughts (Canton et al. 1984; Cowx et al. 1984; Boulton 2003), and macroinvertebrate drift is reduced because of lower stream velocities (Ciborowski et al. 1977). I found significantly lower current velocities and less run habitat available during the drought years. I also observed that a drift feeding species, brown darter (*Etheostoma edwini*), and an insectivore, greater jumprock (*Scartomyzon lachneri*), were found significantly less often in streams during the drought year spring and summers. Therefore, I hypothesize that reductions in swift-water habitat combined with low invertebrate abundances during the drought resulted in the reduction or elimination of these species.

Temperature and dissolved oxygen also can influence stream fish assemblage structure (Cech et al. 1990; Smale and Rabeni 1995). In streams that periodically experience extremes in temperature and dissolved oxygen concentrations, fish assemblages may be dominated by tolerant species, whereas relatively stable streams may contain a more diverse assemblage (Smale and Rabeni 1995). Summer drought conditions such as high water temperatures and low dissolved oxygen concentrations potentially can threaten sensitive species (Lake 2003). In the current study, water temperatures were significantly higher during the drought summer than the non-drought summer, but the mean difference was 1 ^{o}C. I did not detect a difference in dissolved oxygen concentration between drought and non-drought summers. Because most stream fish found in the lower FRB are adapted to warm summer stream temperatures and relatively low dissolved oxygen concentrations (Jenkins and Burkhead 1993), most species probably were not affected by the slightly increased temperatures. However, the lower FRB does contain a few sensitive species, such as redeye chub (*Notropis harperi*), that depend on groundwater inputs for cool water refugia (Metee et al. 1996). In fact, I found significantly fewer redeye chub in summer drought samples. Therefore, increased temperatures may have affected this and other sensitive species during the drought. I believe that drought effects on temperature and dissolved oxygen affected certain sensitive fishes in the lower FRB, but additional habitat factors regulate the presence or abundance of more tolerant species.

Alternatively, the small temperature difference and apparent similarity in dissolved oxygen concentrations between drought and non-drought summers may be an artifact of my sampling protocol. In lower FRB streams, temperature and dissolved oxygen concentrations are known to undergo diel fluctuations with minimum dissolved oxygen occurring before dawn (G. Li; University of Georgia; personal communication). Further, dissolved oxygen fluctuations usually are most severe in summer when water temperatures are warmest (Horne and Goldman 1994), and the fluctuations also may increase in amplitude during drought, which could cause dissolved oxygen to fall to even lower concentrations (Lake 2003). Because I only measured temperature and dissolved oxygen concentration once during each sample, I was unable to observe the diel range of the two parameters. Therefore, dissolved oxygen concentrations were probably lower than I observed and negatively affected fishes in the lower FRB.

Stream fish assemblage structure may vary seasonally. Northern, temperate warmwater stream fishes often migrate downstream to larger, more stable habitats during winter and return in the spring (Hall 1972). In the larger downstream reaches, fishes can conserve energy during the colder months when stream temperatures and metabolism are low by using slow, deep habitats with current blocking structures (Peterson and Rabeni 2001). Warming temperatures and high flow events during spring often trigger large-scale upstream migrations of some adult and larger juvenile fish in northern temperate systems (Hall 1972). These large-scale movements also were reportedly responsible for the recolonization of fish assemblages following large-scale disturbances in northern, temperate streams (Bayley and Osborne 1993). Because lower FRB streams are warmer during the winter than northern, temperate streams, fishes may not need to overwinter in downstream reaches and may not undertake large-scale seasonal movements. Nonetheless, species richness was higher following resumption of normal streamflows during the non-drought spring. Additionally, the significantly higher species richness and biomass during the non-drought summer suggests that fishes remained in smaller streams throughout the summer. Thus, large-scale, seasonal fish movement probably is the mechanism by which lower FRB fish assemblages recovered from the drought.

Reproduction and juvenile recruitment also contribute to fish assemblage recovery following droughts in other areas (Larimore et al. 1959; Stanley et al. 1997; Matthews 1998; Gasith and Resh 1999; Labbe and Fausch 2000). In the present study, biomass was greater during the non-drought summer than during the drought summers in small streams. The greater biomass was related to greater fish mass rather than fish crowding because more space was available during the non-drought summer than during the drought summers. Although the presence of older and large-bodied fishes was responsible for a portion of this increase, young-of-year and small fish are generally among the most abundant fishes and account for the greatest portion of biomass and production in small streams (Mann 1971; Mathews 1971; Mahon et al. 1979; Peterson 1996). Consequently, much of the increase in fish mass during the non-drought summer probably was related to increased reproduction, growth, and recruitment of juvenile fishes.

The drought played a major role in structuring fish assemblages in the lower FRB. However, other factors also influenced fish assemblages regardless of drought conditions. For example, species richness, biomass, and IBI were greater in small, groundwater influenced streams than in small, surface water dominated streams during both drought and non-drought winters. Mean water temperatures in groundwater-influenced streams were 5 ^{o}C greater than surface water dominated streams during winter. These results are similar to previous studies that suggest groundwater influenced streams generally contain warmer water than surface water dominated streams and can serve as areas of thermal refugia for warmwater stream fishes (Peterson and Rabeni 1996). Because fishes in thermally enhanced areas usually are more active and can feed more frequently than conspecifics in colder habitats (Diana 1995; Peterson and Rabeni 1996), fishes in the lower FRB possibly benefit energetically from using thermally-enhanced, groundwater-influenced streams during the winter.

In addition to warm water during the winter, groundwater influenced streams in the lower FRB also contain relatively high levels of calcium bicarbonate, which originates from the underlying Ocala Limestone (Hicks et al. 1987). Calcium bicarbonate causes increased water hardness and conductivity, which have been related to increased stream fish productivity in other studies (Scarnecchia and Bergersen 1987; Waters et al. 1993; Kwak and Waters 1997). In the present study, biomass was higher in small, groundwater-influenced streams than in small, surface water dominated streams during the non-drought year spring and in all years during summer. Thus, groundwater-influenced streams in the lower FRB are probably more productive than surface water dominated streams throughout the year.

Management Implications

This and other studies suggest that fish movement is sufficient for natural recolonization of streams affected by drought or other disturbances, provided that species have access to the affected reaches and that habitats return to previous conditions (Bayley and Osborne 1993; Peterson and Bayley 1993). Stream fragmentation, however, could inhibit natural recolonization and the ability of lower FRB stream fishes to recover from disturbance. Fragmentation occurs when streams are divided into two or more sections, which can cause isolation of stream-fish populations (Primack 1998). Reservoirs probably are the most common causes of stream fragmentation because they can impede fish migrations (Porto et al. 1999; Beasley and Hightower 2000). Fish assemblages within the inundated stream channel of a reservoir often differ from those in the upstream reaches of tributaries (Patriarche and Campbell 1958; Baxter 1977; Martinez et al. 1994). Thus, the species pool available for recolonization probably would be insufficient for complete recovery in the event of a catastrophic disturbance (e.g., severe drought) in the stream reach above a reservoir. Recent studies have shown that lower FRB fish assemblages are significantly, negatively influenced by fragmentation (Peterson et al. 2004). Therefore, managers should consider the importance of stream connectivity for maintaining native fish assemblage structure in the lower FRB when developing natural resource management plans.

Groundwater-influenced streams seem to be important areas for lower FRB stream fish assemblages. Groundwater-influenced streams support higher fish biomass during spring and summer months than surface water dominated streams, and groundwater-influenced streams also may offer thermal refugia during winter. The increased biomass in groundwater-influenced streams suggests they could potentially function as population sources, and their degradation or elimination could have cascading effects throughout the entire lower FRB. For example, these streams could produce abundant prey populations for economically important sport fishes such as shoal bass (*Micropterus cataractae*) and flathead catfish (*Pylodictis olivaris*). Groundwater levels in the Floridan Aquifer maintain baseflow in lower FRB streams during summer months, but levels can be severely reduced by pumping for agricultural irrigation, municipal water supply, and industrial uses (Hicks et al. 1987). Further, lack of recharge and extensive use during drought can cause additional groundwater reductions that ultimately result in streambed desiccation (Mosner 2002). Thus, groundwater quantity and quality must be maintained, especially during drought conditions, so that groundwater influenced streams can continue to serve as refugia and maintain high levels of fish biomass.

Droughts and other naturally occurring disturbances are important factors that influence stream fish assemblage structure (Resh et al. 1988; Grossman et al. 1998). As water resources in the lower FRB and the Southeast face an increasing demand because of high population growth, focus often is placed on minimum instream flow standards (i.e., lowest streamflows that can maintain aquatic life). However, long-term effects of persistent, low streamflows may have permanent, negative effects on stream fish assemblage structure. Although stream fish can recover from low streamflows, relatively high flows are required for natural seasonal patterns of movement and recolonization. Thus, protection of aquatic biota in the Southeast and the lower FRB will benefit from management decisions based on streamflow models that incorporate both spatial (e.g., fragmentation) and temporal components for evaluating long-term (e.g., chronic, cumulative) effects of flow policies.

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Table 1. Name, location, physiographic district, groundwater designation, and stream link magnitude of sample sites in the lower Flint River Basin. GW indicates groundwater influenced streams, and SW indicates surface water dominated streams.

Site Code	Creek Name	County	Physiographic District	Latitude	Longitude	Groundwater Designation	Link Magnitude
BEAR	Bear Creek	Webster	Fall Line Hills	N 31.99368	W 84.59502	SW	29
CART	Carter Creek	Randolph	Fall Line Hills	N 31.63665	W 84.72050	SW	70
CHIC1	Chickasawhatchee Creek	Terrell	Fall Line Hills	N 31.70462	W 84.38927	GW	48
CHIC2	Chickasawhatchee Creek	Dougherty	Dougherty Plain	N 31.59392	W 84.45200	GW	137
CHIC3	Chickasawhatchee Creek	Baker	Dougherty Plain	N 31.38775	W 84.46601	GW	215
COOL1	Cooleewahee Creek	Dougherty	Dougherty Plain	N 31.58698	W 84.26352	GW	2
COOL2	Cooleewahee Creek	Baker	Dougherty Plain	N 31.33087	W 84.33049	GW	22
ICH1	Ichawaynochaway Creek	Terrell	Fall Line Hills	N 31.82581	W 84.56720	SW	52
ICH2	Ichawaynochaway Creek	Calhoun	Dougherty Plain	N 31.52796	W 84.58271	SW	294
ICH3	Ichawaynochaway Creek	Baker	Dougherty Plain	N 31.38299	W 84.54643	GW	636
KIN1	Kinchafoonee Creek	Webster	Fall Line Hills	N 32.12701	W 84.59275	SW	334
KIN2	Kinchafoonee Creek	Webster	Fall Line Hills	N 32.05403	W 84.54886	SW	401
KIN3	Kinchafoonee Creek	Lee	Fall Line Hills	N 31.76604	W 84.25425	SW	807
LIME	Lime Creek	Sumter	Fall Line Hills	N 32.03508	W 83.99265	GW	132
MILL	Mill Creek	Worth	Dougherty Plain	N 31.66842	W 83.99644	GW	105
MUC1	Muckalee Creek	Schley	Fall Line Hills	N 32.20615	W 84.41703	GW	61
MUC2	Muckalee Creek	Lee	Fall Line Hills	N 31.73141	W 84.12495	GW	425
MUC3	Muckalee Creek	Lee	Dougherty Plain	N 31.89573	W 84.19830	GW	511
SPR	Spring Creek	Miller	Dougherty Plain	N 31.07521	W 84.71867	GW	319

Table 2. Mean stream width, depth, and velocity of habitat samples taken in lower FRB streams during winter, spring, and summer of drought and non-drought years.

	Winter		Spring		Summer	
Habitat Parameter	Drought	Non-drought	Drought	Non-drought	Drought	Non-drought
Mean Width (m)	13.67	12.58	11.59	13.96	11.72	13.87
Mean Depth (m)	0.62	0.72	0.42	0.70	0.47	0.70
Mean Velocity (m/s)	0.18	0.21	0.10	0.22	0.13	0.21

Table 3. Description of habitat categories and ranges used for measuring stream habitat diversity in lower FRB streams during all seasons of 2001, 2002, and 2003.

	Category Number and Description					
Measurement	1	2	3	4	5	6
Depth (m)	0	0.001 - 0.06	0.06 - 0.14	0.14 - 0.22	0.22 - 0.32	> 0.32
Velocity (m/s)	0 - 0.2	0.2 - 0.35	0.35 - 0.48	0.48 - 0.63	0.63 - 0.91	> 0.91

Table 4. Description of site-specific model parameters used to evaluate the fish assemblages in the lower FRB during 2001, 2002, and 2003 sampling.

Parameter	Description of Model Parameter
LK[a]	Link magnitude
AREA[b]	Area (m^2) of sample site
DT	Drought; Binary coded as 1 for drought conditions, 0 for non-drought
GW	Groundwater; Binary coded as 1 for groundwater influenced, 0 for surface water dominated
H_P	Habitat diversity of sample site
LWD	Large wood density (pieces/m^2)
LK*DT	Link magnitude*drought interaction
LK*GW	Link magnitude*groundwater interaction
LK*H_P	Link magnitude*habitat diversity interaction
DT*H_P	Drought*habitat diversity interaction
DT*GW	Drought*groundwater interaction
GW*H_P	Groundwater*habitat diversity interaction

[a] Link magnitude was included in every model

[b] Area was only included in species richness, fish species diversity, and Index of Biotic Integrity models

Table 5. Number of sites sampled and below 7Q10 throughout the study in the lower Flint River Basin[a].

Year	Season	Number of Sites Sampled	Number of Sites Below Monthly 7Q10 (%)
2001	Summer	19	15 (79%)
2002	Winter	18	11 (61%)
	Spring	19	19 (100%)
	Summer	19	9 (47%)
2003	Winter	11	1 (9%)
	Spring	17	0 (0%)
	Summer	17	0 (0%)

[a] Estimates based on significant discharge relationships with USGS gauge 02353500 at Ichawaynochaway Creek, Milford, Georgia.

Table 6. Fish abundance, gear efficiency-adjusted fish abundance estimates, number of species, and number of families sampled in lower FRB streams during all seasons of 2001, 2002, and 2003.

Year	Season	Abundance	Adjusted Abundance	Species	Families
2001	Summer	2485	37,968	42	13
2002	Winter	2799	46,569	42	14
	Spring	3048	39,174	44	14
	Summer	3317	43,764	47	16
2003	Winter	2444	84,561	42	12
	Spring	2944	52,941	51	14
	Summer	4433	86,867	40	13

Table 7. Matched pairs *t*-test results for standardized mesohabitat area measured in lower FRB streams during 2001, 2002, and 2003.

Season	Mesohabitat	DF	*t-value*	*p-value*
Winter	Edgewater	10	-1.028	0.328
	Side channel	1	-4.074	0.153
	Pool	10	-2.925	0.015
	Riffle	0		
	Run	10	3.444	0.006
	Race	10	-1.273	0.232
Spring	Edgewater	16	1.048	0.310
	Side channel	5	-0.989	0.368
	Pool	16	-2.381	0.030
	Riffle	2	-2.514	0.128
	Run	16	5.673	<0.001
	Race	16	0.918	0.372
Summer	Edgewater	33	2.390	0.023
	Side channel	14	-2.062	0.058
	Pool	33	-0.928	0.360
	Riffle	6	-5.896	0.001
	Run	33	4.237	<0.001
	Race	33	3.158	0.003

Table 8. Matched pairs *t*-test results for dissolved oxygen (DO), turbidity, and water temperature (Water temp) measurements taken in lower FRB streams during 2001, 2002, and 2003. Positive differences indicate higher values in the non-drought year, and negative differences indicate higher values in drought years.

Season	Parameter	DF	Mean Difference	90 % Confidence Interval		*t-value*	*P-value*
Winter	DO (mg/L)	10	3.39	1.22	5.57	2.824	0.018
	Turbidity (NTU)	10	2.96	-0.85	6.77	1.407	0.190
	Water temp (^{o}C)	10	-3.13	-4.96	-1.29	-3.085	0.012
Spring	DO (mg/L)	16	0.77	0.01	1.53	1.760	0.098
	Turbidity (NTU)	15	12.52	8.91	16.13	6.081	< 0.001
	Water temp (^{o}C)	16	0.71	-0.87	2.28	0.781	0.446
Summer	DO (mg/L)	29	-0.49	-0.99	0.00	-1.692	0.101
	Turbidity (NTU)	33	18.62	14.65	22.60	7.933	< 0.001
	Water temp (^{o}C)	32	-1.22	-1.98	-0.47	-2.735	0.010

Table 9. Estimates of fixed and random effects for the best fitting hierarchical linear models predicting natural log-transformed species richness in lower FRB streams during winter, spring, and summer.

				90% Confidence Interval	
Season	Parameter	Parameter estimate	Standard error	Lower	Upper
Winter	Intercept	2.2014	0.1089	2.0112	2.3915
	Link	-0.0011	0.0003	-0.0018	-0.0005
	Drought	-0.3663	0.1391	-0.6213	-0.1114
	Link*Drought	0.0017	0.0004	0.0009	0.0025
	Random effect	0.0060	0.0443	-0.0666	0.0785
Spring	Intercept	3.0062	0.0800	2.8670	3.1453
	Link	0.0008	0.0002	0.0005	0.0011
	Drought	-0.2504	0.0841	-0.3925	-0.1083
	Random effect	<0.0001			
Summer	Intercept	3.0062	0.0800	2.8670	3.1453
	Link	0.0008	0.0002	0.0005	0.0011
	Drought	-0.2504	0.0841	-0.3925	-0.1083
	Random effect	<0.0001			

Table 10. Akaike importance weights for parameters from candidate models predicting natural log-transformed species richness in lower FRB streams during winter, spring, and summer. Explanations of model parameters can be found in Table 4.

		Importance Weights[b]		
Model Parameter[a]	Number of Models	Winter	Spring	Summer
Drought	30	**0.40**	**0.83**	**0.79**
Drought*Habitat diversity	4	0.00	0.01	**0.12**
Groundwater	32	**0.90**	**0.36**	0.28
Groundwater*Drought	4	0.02	0.03	0.02
Groundwater*Habitat diversity	4	0.01	0.00	0.00
Habitat diversity	30	0.19	0.19	**0.35**
Link*Drought	8	0.03	0.10	**0.16**
Link*Groundwater	8	**0.52**	0.09	0.09
Link*Habitat diversity	6	0.02	0.01	0.02
Large wood density	18	0.12	**0.23**	0.15
Sample site area	28	**0.51**	**0.33**	**0.61**

[a] Intercept and link magnitude were included in all models; hence, importance weights equal 1.

[b] Importance weights in bold indicate that the parameter was estimated in analysis.

Table 11. Estimates of fixed and random effects for the best fitting hierarchical linear models predicting fish species diversity in lower FRB streams during winter, spring, and summer.

Season	Parameter	Parameter estimate	Standard error	90% Confidence Interval Lower	90% Confidence Interval Upper
Winter	Intercept	2.2014	0.1089	2.0112	2.3915
	Link	-0.0011	0.0003	-0.0018	-0.0005
	Drought	-0.3663	0.1391	-0.6213	-0.1114
	Link*Drought	0.0017	0.0004	0.0009	0.0025
	Random effect	0.0060	0.0443	-0.0666	0.0785
Spring	Intercept	0.6990	0.3782	0.0410	1.3569
	Link	0.0047	0.0012	0.0026	0.0069
	Habitat diversity	0.5406	0.1457	0.2840	0.7971
	Link*Habitat diversity	-0.0015	0.0004	-0.0022	-0.0008
	Sample site area	-0.1855	0.0765	-0.3202	-0.0507
	Random effect	0.0025	0.0189	-0.0285	0.0334
Summer	Intercept	1.6282	0.2204	1.2448	2.0116
	Link	<0.0001	0.0002	-0.0003	0.0003
	Habitat diversity	0.1972	0.0747	0.0708	0.3235
	Large wood density	-2.6080	1.3383	-4.8709	-0.3451
	Random effect	<0.0001			

Table 12. Akaike importance weights for parameters from candidate models predicting fish species diversity in lower FRB streams for all seasons. Explanations of model parameters can be found in Table 4.

		Importance Weights[b]		
Model Parameter[a]	Number of Models	Winter	Spring	Summer
Drought	30	**0.68**	0.34	0.21
Drought*Habitat diversity	4	<0.01	0.03	0.01
Groundwater	32	**0.26**	0.27	0.26
Groundwater*Drought	4	0.01	0.01	0.00
Groundwater*Habitat diversity	4	0.01	0.00	0.00
Habitat diversity	30	0.23	**0.53**	**0.92**
Link*Drought	8	**0.57**	0.05	0.02
Link*Groundwater	8	0.01	0.02	0.02
Link*Habitat diversity	6	0.05	**0.39**	0.07
Large wood density	18	0.07	0.13	**0.62**
Sample site area	28	**0.33**	**0.49**	0.25

[a] Intercept and link magnitude were included in all models; hence, importance weights equal 1.

[b] Importance weights in bold indicate that the parameter was estimated in analysis.

Table 13. Estimates of fixed and random effects for the best fitting hierarchical linear models predicting natural log-transformed biomass in lower FRB streams during winter, spring, and summer.

				90% Confidence Interval	
Season	Parameter	Parameter estimate	Standard error	Lower	Upper
Winter	Intercept	6.1356	1.5764	3.3720	8.8992
	Link	-0.0005	0.0007	-0.0018	0.0007
	Groundwater	-5.4867	1.5637	-8.3532	-2.6201
	Habitat diversity	-1.5443	0.5514	-2.5550	-0.5336
	Groundwater*Habitat diversity	2.4724	0.5818	1.4059	3.5390
	Random effect	0.0476	0.1310	-0.1672	0.2623
Spring	Intercept	3.0605	0.2605	2.6073	3.5136
	Link	<0.0001	0.0008	-0.0014	0.0014
	Random effect	0.3440	0.2148	-0.0084	0.6963
Summer	Intercept	2.1560	0.3160	1.6020	2.7101
	Link	0.0015	0.0008	0.0001	0.0029
	Groundwater	1.2643	0.3961	0.5955	1.9331
	Link*Groundwater	-0.0033	0.0012	-0.0053	-0.0014
	Random effect	<0.0001			

Table 14. Akaike importance weights for parameters from candidate models predicting natural lot-transformed biomass in lower FRB streams for all seasons. Explanations of model parameters can be found in Table 4.

		Importance Weight[b]		
Model Parameter	Number of Models	Winter	Spring	Summer
Drought	15	**0.19**	**0.37**	**0.42**
Drought*Habitat diversity	2	0.00	0.00	0.02
Groundwater	16	**0.97**	**0.63**	**0.90**
Groundwater*Drought	2	**0.07**	**0.12**	0.03
Groundwater*Habitat diversity	2	**0.55**	0.02	0.02
Habitat diversity	15	**0.63**	0.24	**0.30**
Link*Drought	4	0.02	0.02	**0.09**
Link*Groundwater	4	**0.30**	**0.15**	**0.81**
Link*Habitat diversity	3	0.00	0.03	0.02
Large wood density	9	0.02	0.20	0.03

[a] Intercept and link magnitude were included in all models; hence, importance weights equal 1.
[b] Importance weights in bold indicate that the parameter was estimated in analysis.

Table 15. Chi-square statistics, odds ratios (OR), and OR confidence intervals of species whose frequencies of occurrence were significantly different between drought and non-drought years during spring and summer.

Season	Common Name	Scientific Name	χ^2	*P-value*	OR	90 % Confidence Interval Lower	90 % Confidence Interval Upper
Spring	Bowfin	*Amia calva*	3.184	0.074	0.2157	0.049	0.953
	Clear chub	*Hybopsis winchelli*	4.760	0.029	5.1852	1.426	18.853
	Largemouth bass	*Micropterus salmoides*	3.567	0.059	0.2381	0.065	0.866
	Redear Sunfish	*Lepomis microlophus*	2.786	0.095	0.3182	0.101	0.999
	Redfin pickerel	*Esox americanus*	4.360	0.037	0.2238	0.067	0.752
	Warmouth	*Lepomis gulosus*	5.969	0.015	0.1324	0.031	0.574
Summer	Bowfin	*Amia calva*	8.746	0.003	0.1225	0.034	0.440
	Brown darter	*Etheostoma edwini*	11.069	0.001	0.0794	0.019	0.336
	Greater jumprock	*Scartomyzon lachneri*	4.844	0.028	0.2157	0.065	0.720
	Redeye chub	*Notropis harperi*	6.896	0.009	0.1681	0.051	0.552
	Swamp darter	*Etheostoma fusiforme*	4.223	0.040	4.8913	1.264	18.928
	Warmouth	*Lepomis gulosus*	5.298	0.021	0.2518	0.091	0.693

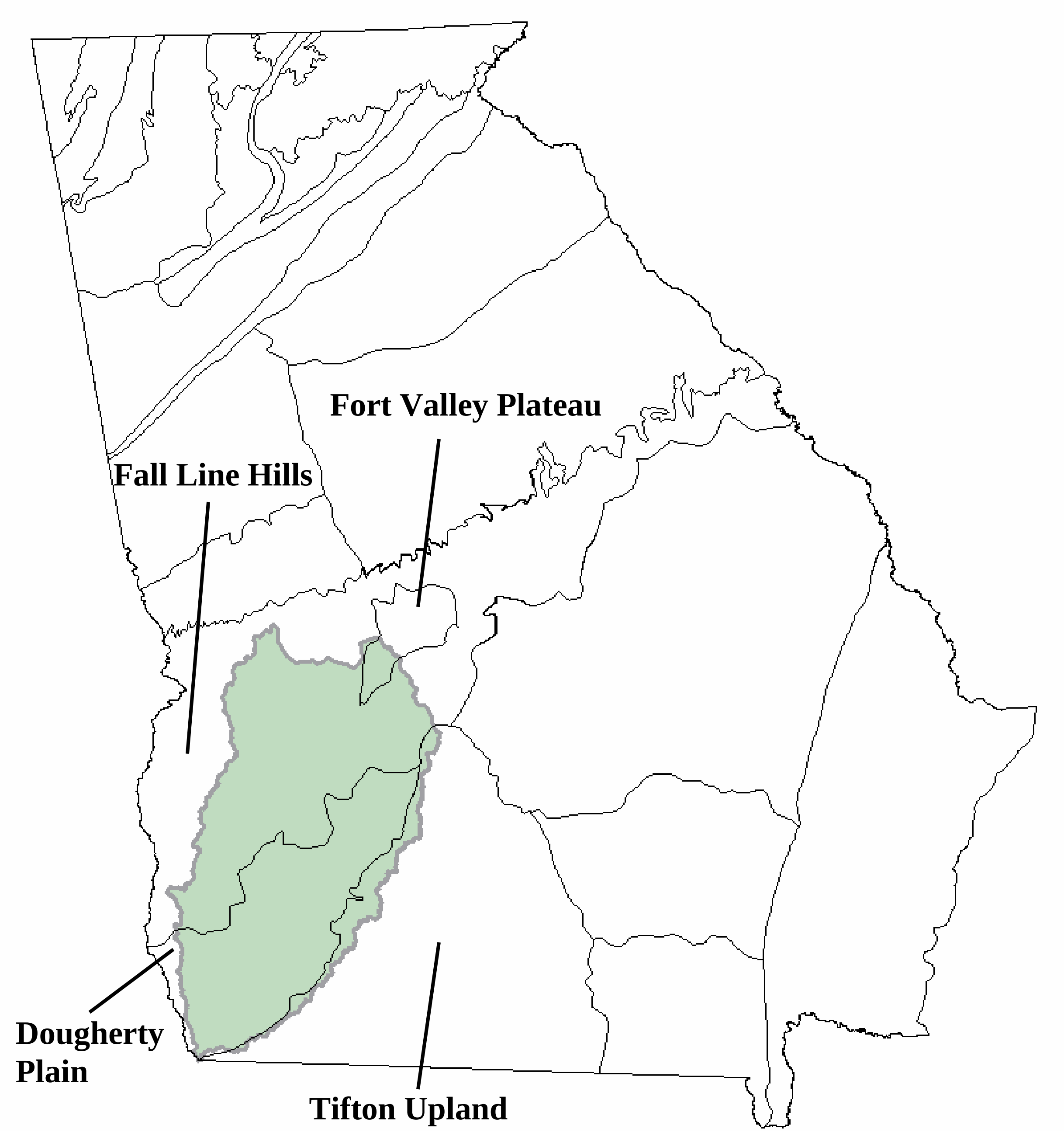

Figure 1. Location of the lower Flint River Basin within the physiographic districts in Georgia. The lower Flint River Basin is shaded, and the physiographic districts are outlined. (Adapted from Clark and Zisa 1976).

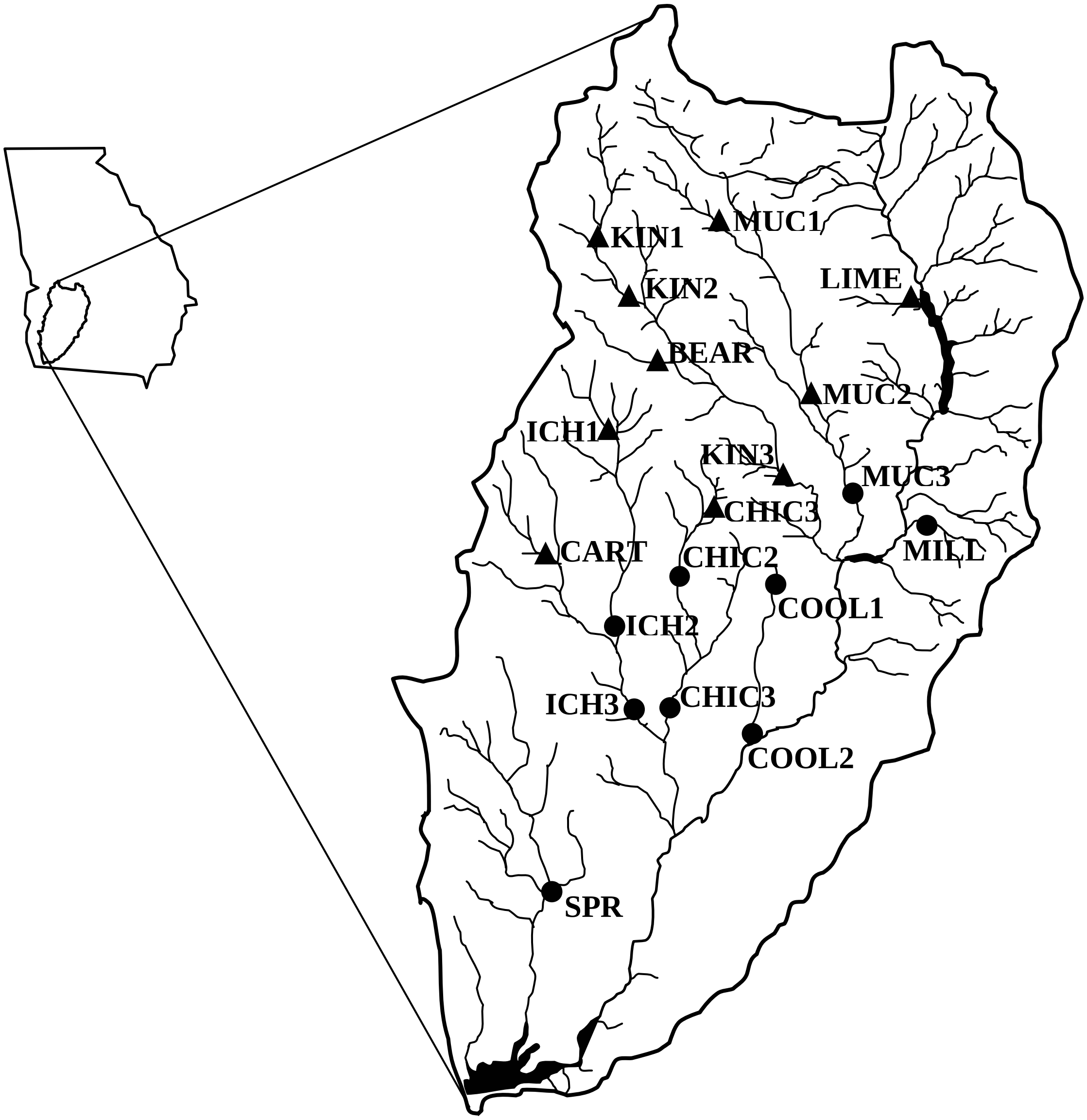

Figure 2. Locations of sample sites in the lower Flint River Basin of southwestern Georgia that were sampled during 2001, 2002, and 2003. Dougherty Plain sites are marked with closed circles, and Fall Line Hills sites are marked with closed triangles. Sites are labeled with abbreviations that can be found in Table 1.

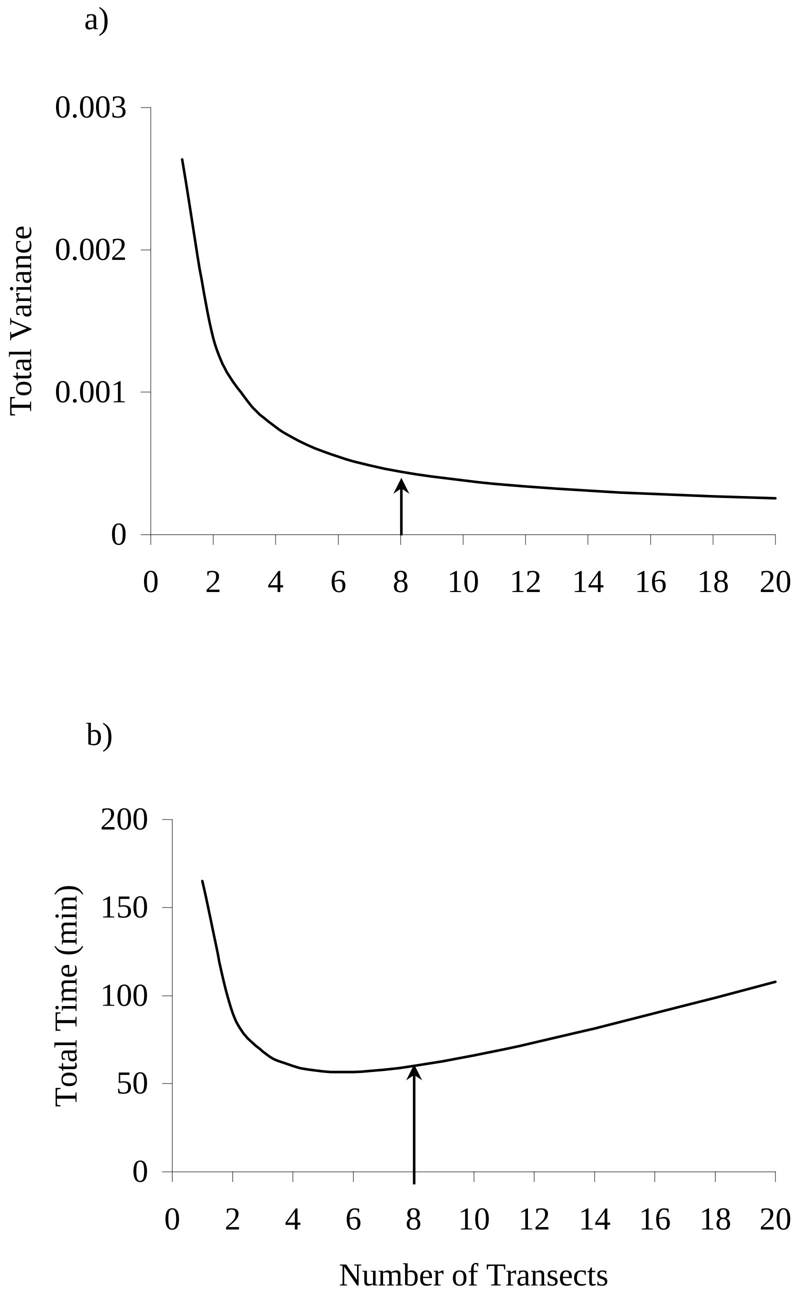

Figure 3. Estimated a) total variance and b) total time when mean current velocity was measured at 80 points along various numbers of transects in lower FRB streams during summer 2001. Optimal sampling strategy, shown by the arrows, occurs when measurements are taken at 8 points along 10 transects. These trends are similar for all habitat parameters.

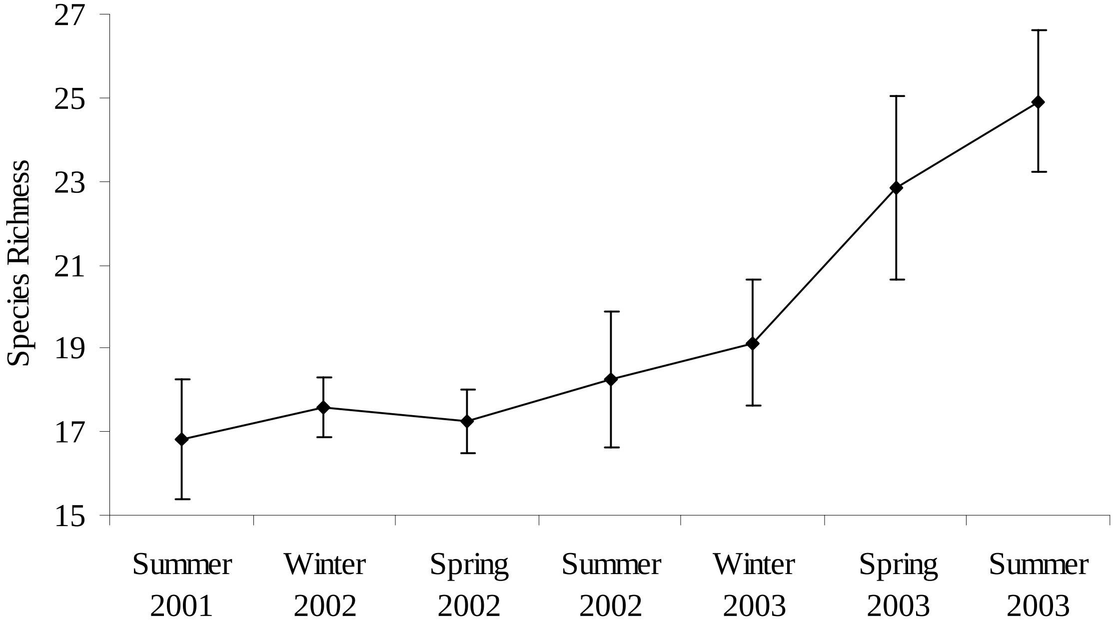

Figure 4. Adjusted species richness values from small (link magnitude < 300) lower FRB streams during 2001, 2002, and 2003. Vertical bars indicate plus/minus one standard deviation.

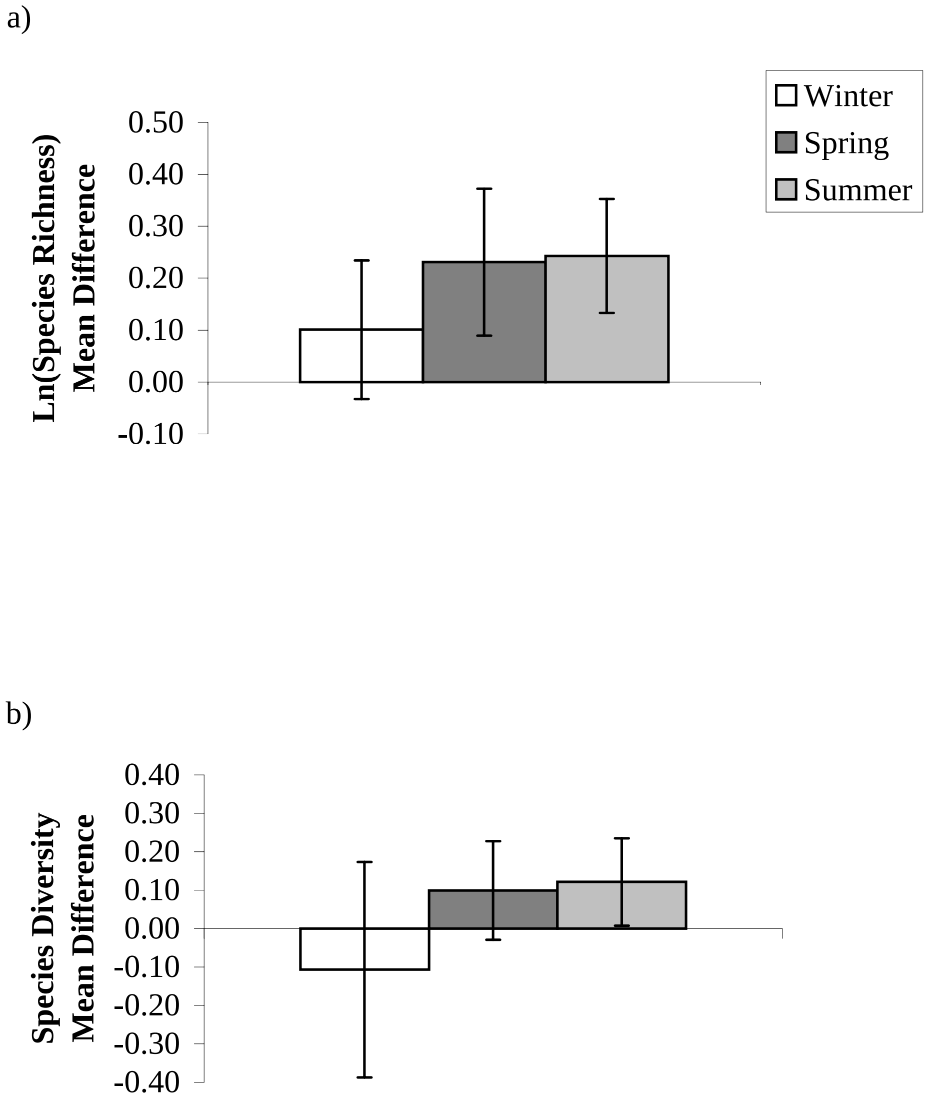

Figure 5. Mean difference in a) species richness and b) fish species diversity between non-drought and drought years during winter, spring, and summer in lower FRB streams. Vertical lines represent 90% confidence intervals. Positive differences indicate higher values during non-drought conditions, while negative differences indicate higher values during drought conditions.

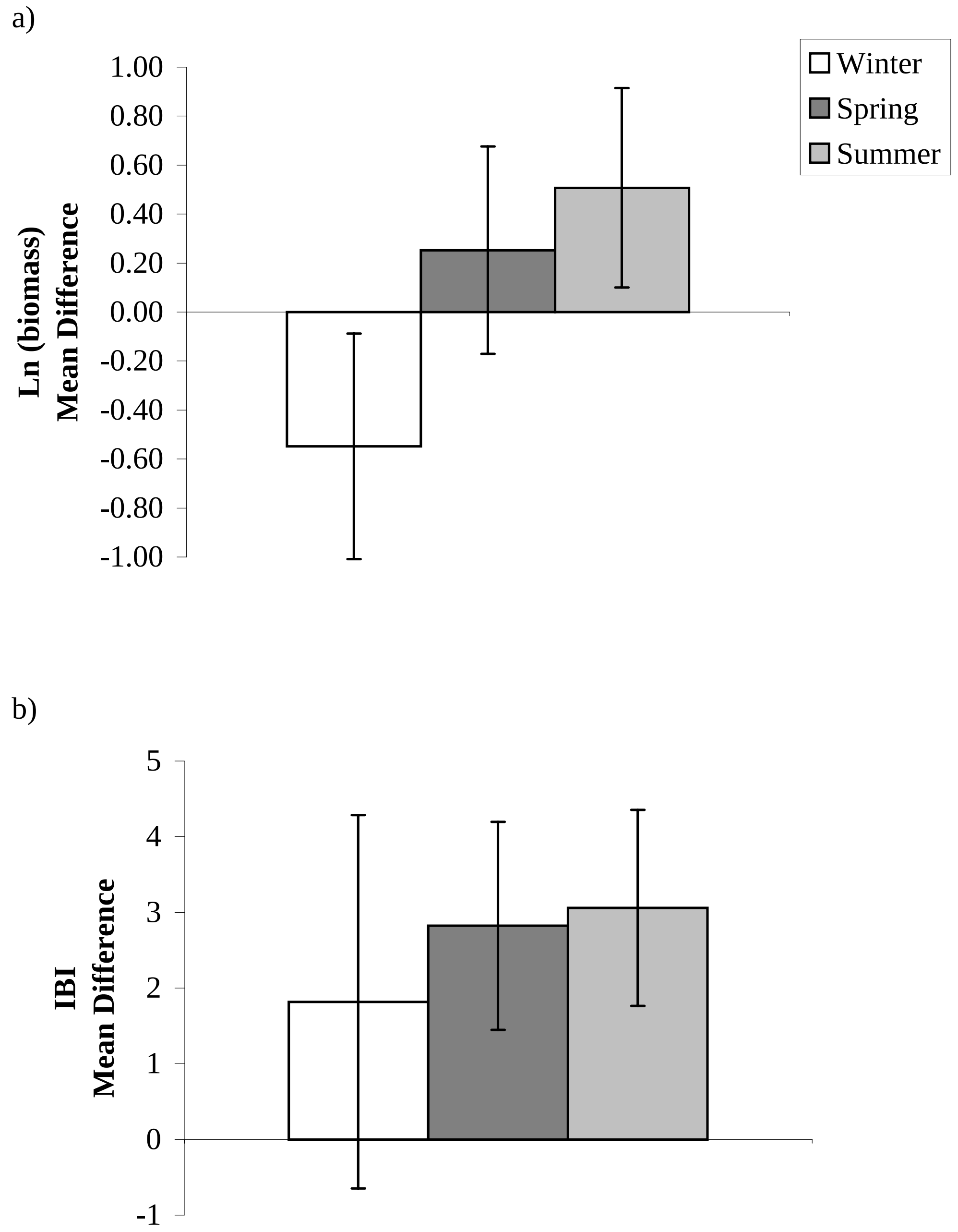

Figure 6. Mean difference in a) biomass (kg/ha) and b) Index of Biotic Integrity between non-drought and drought years during winter, spring, and summer in lower FRB streams. Vertical lines represent 90% confidence intervals. Positive differences indicate higher values during non-drought conditions, while negative differences indicate higher values during drought conditions.

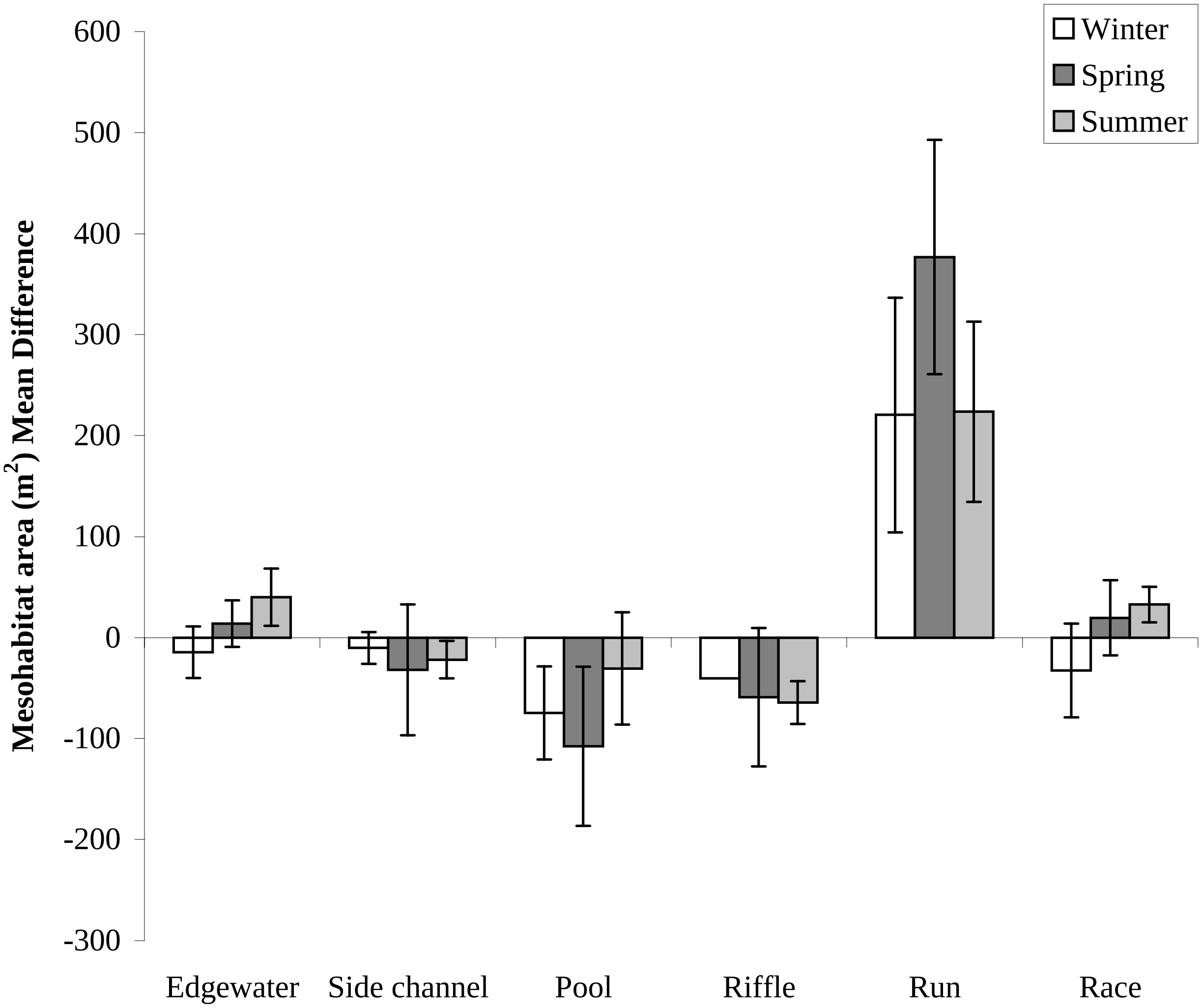

Figure 7. Mean difference in standardized mesohabitat area between non-drought and drought years for winter, spring, and summer in lower FRB streams. Vertical lines indicate 90% confidence intervals. Positive differences indicate higher values during non-drought conditions, while negative differences indicate higher values during drought conditions.

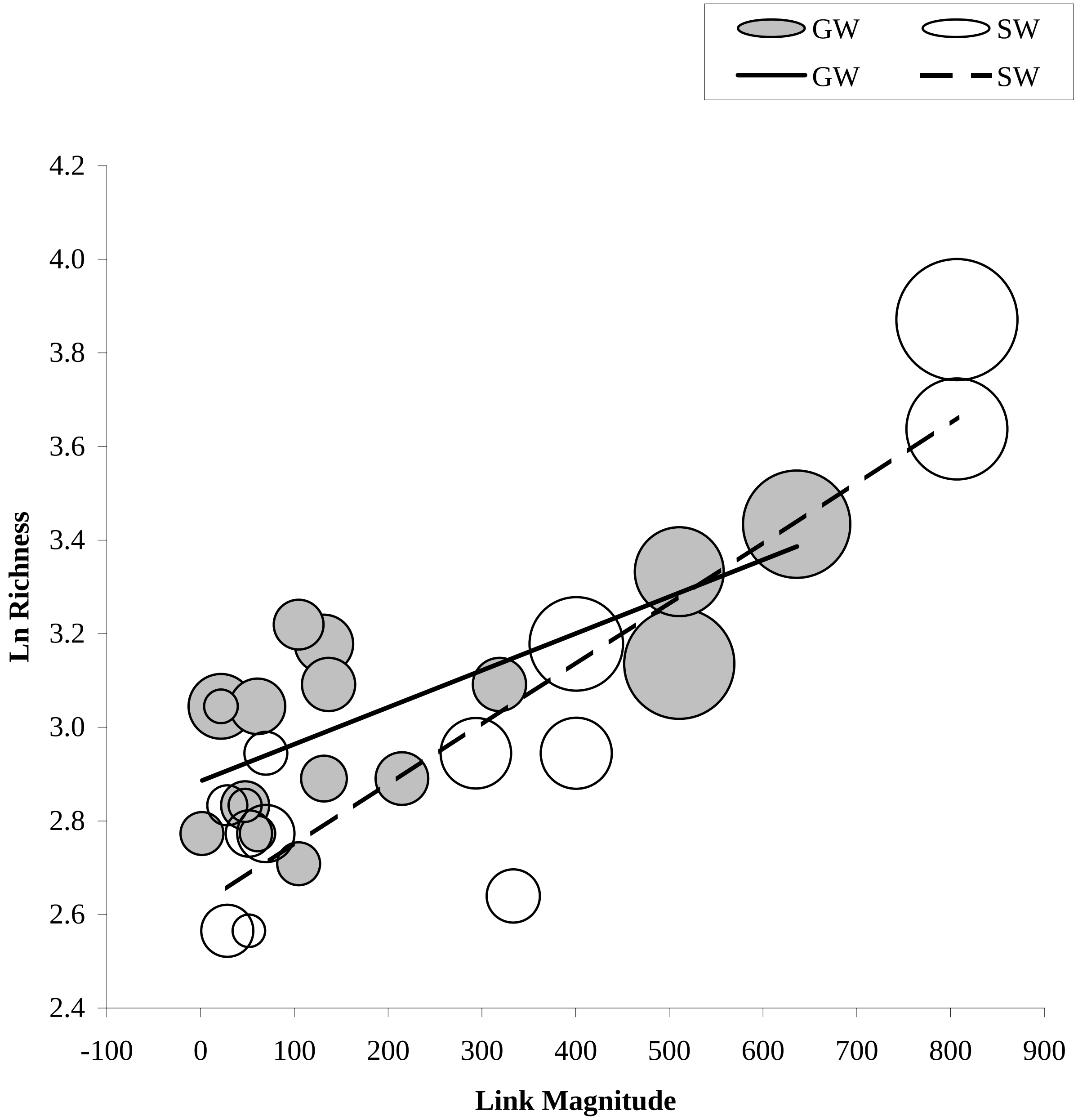

Figure 8. Relationship between link magnitude, groundwater, sample site area, and species richness in lower FRB streams during winter. Shaded circles represent groundwater influenced (GW) sample sites and open circles represent surface water dominated (SW) sample sites. Circle size indicates sample site area. Solid and dashed lines represent model predictions.

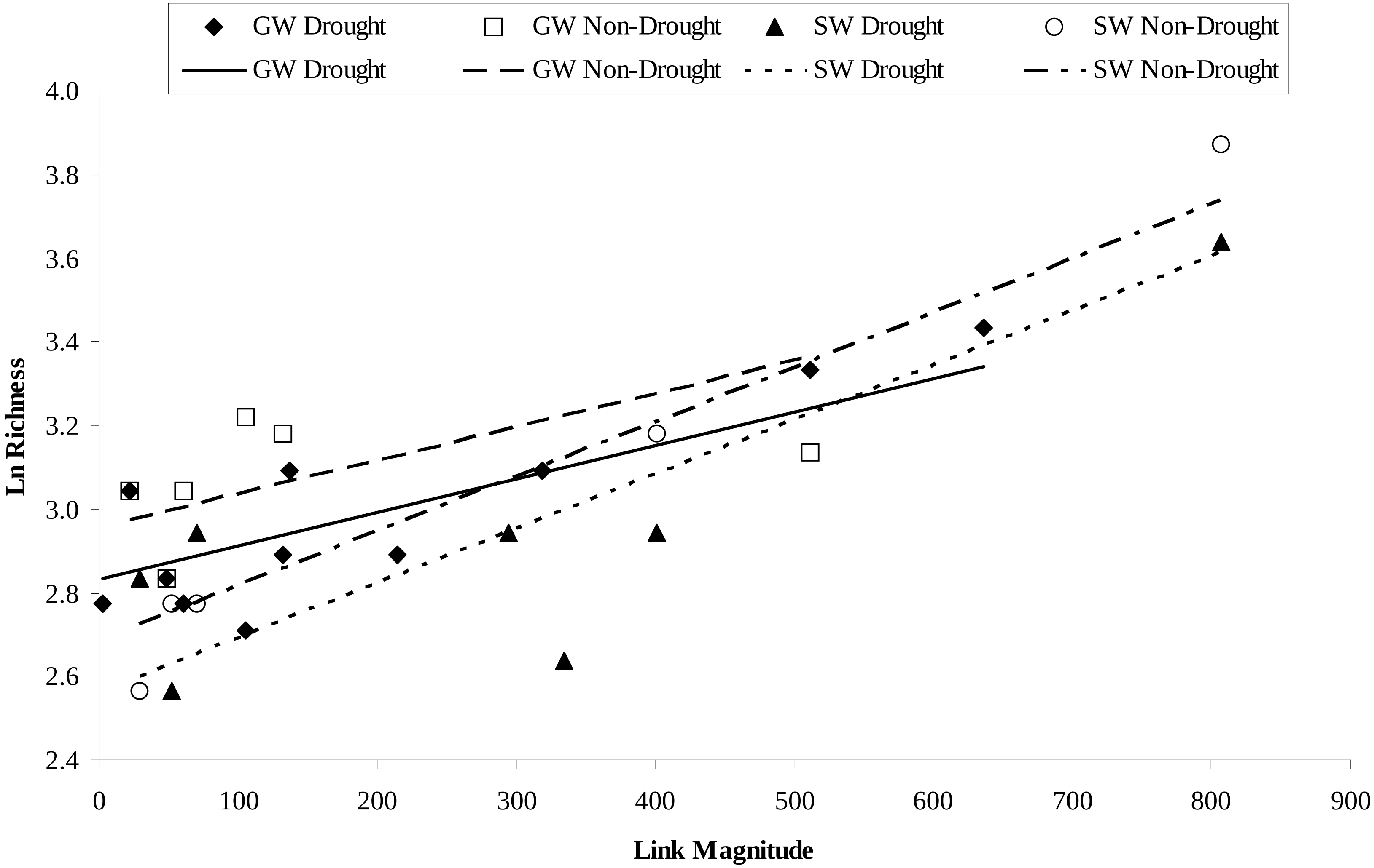

Figure 9. Relationship between link magnitude, groundwater, drought, and species richness in lower FRB streams during winter. GW indicates groundwater influenced sites, and SW indicates surface water dominated sites. Solid and dashed lines represent model predictions.

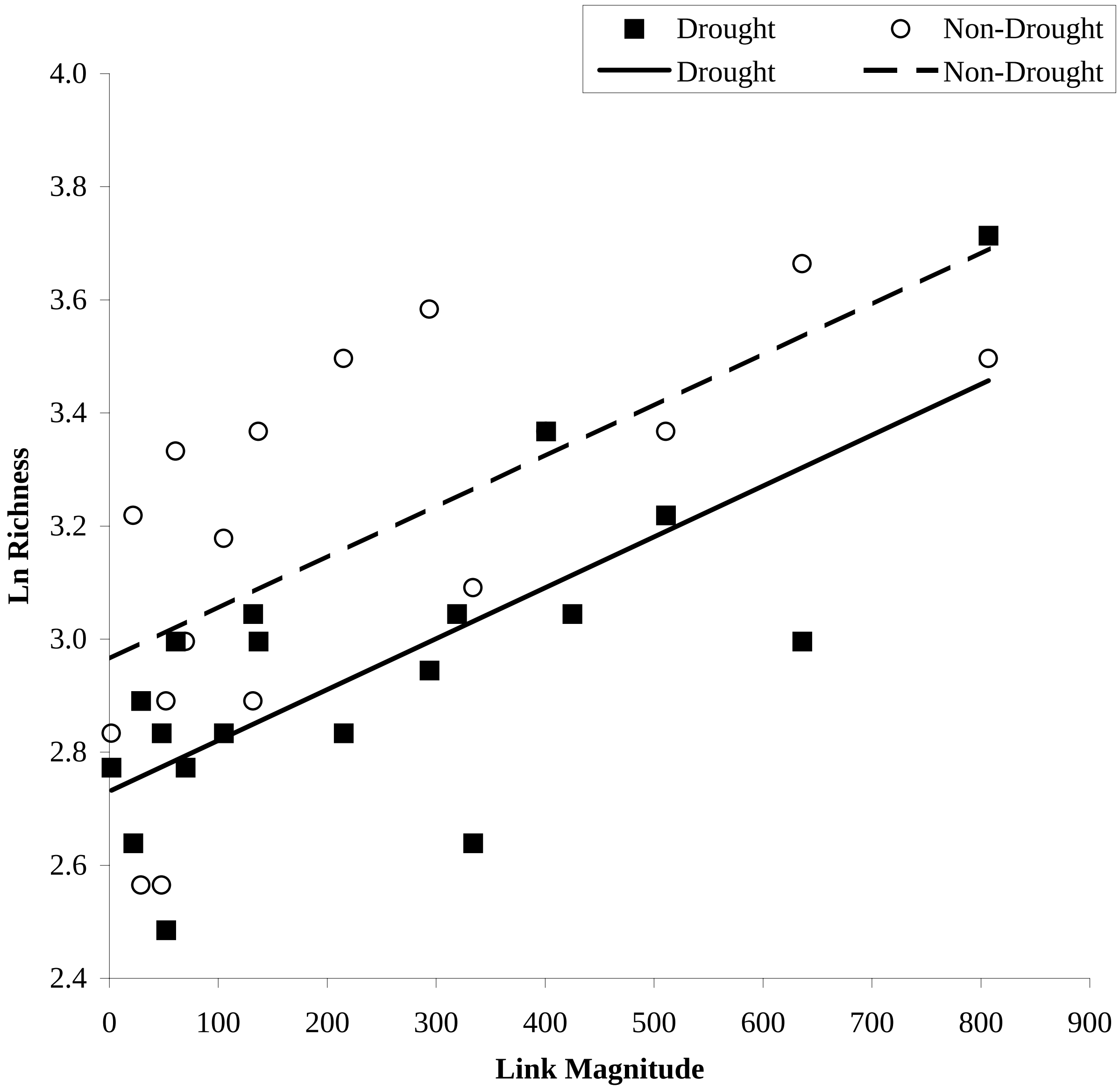

Figure 10. Relationship between link magnitude, drought, and species richness in lower FRB streams during spring. Solid and dashed lines represent model predictions.

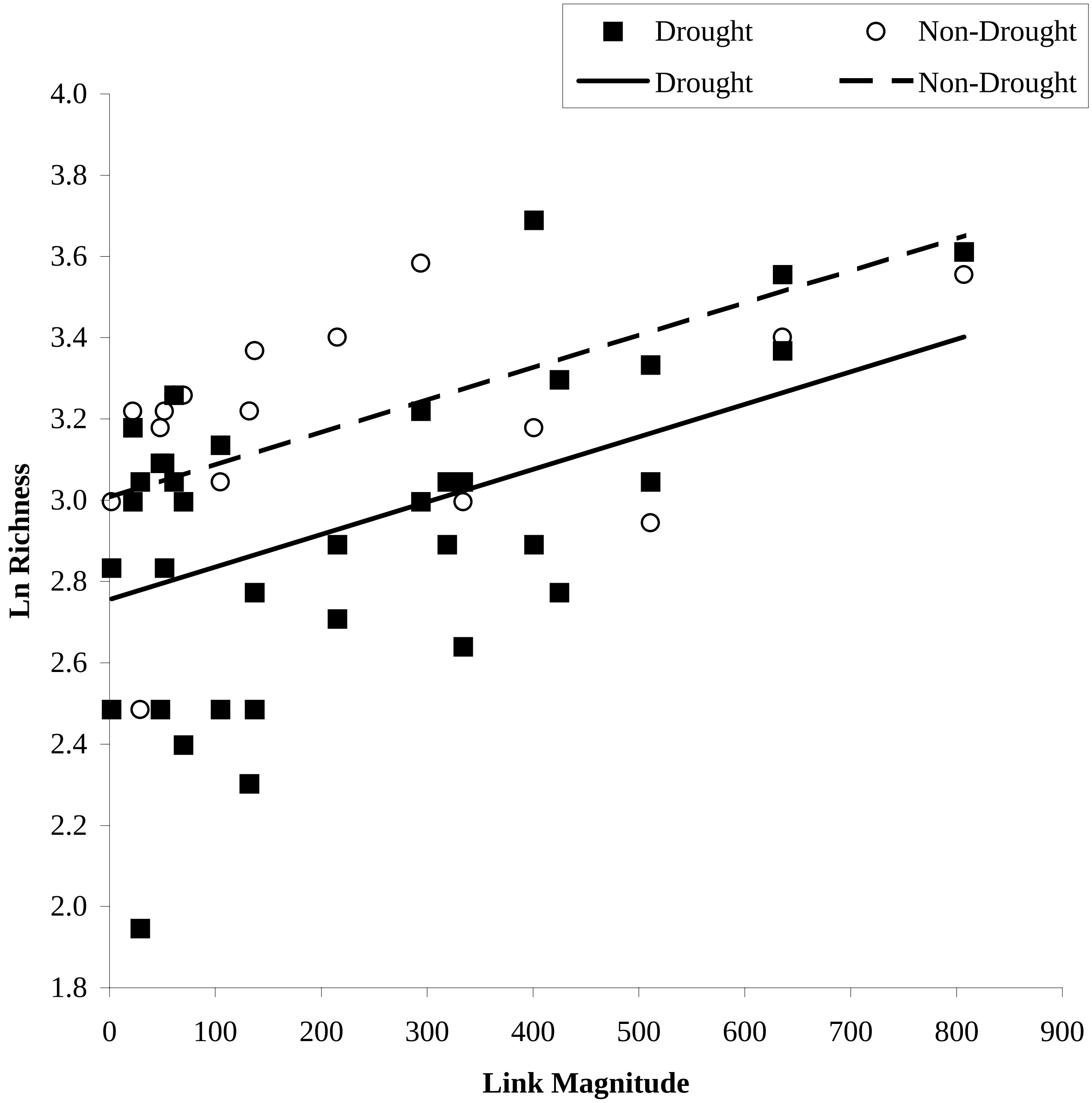

Figure 11. Relationship between link magnitude, drought, and species richness in lower FRB streams during summer. Solid and dashed lines represent model predictions.

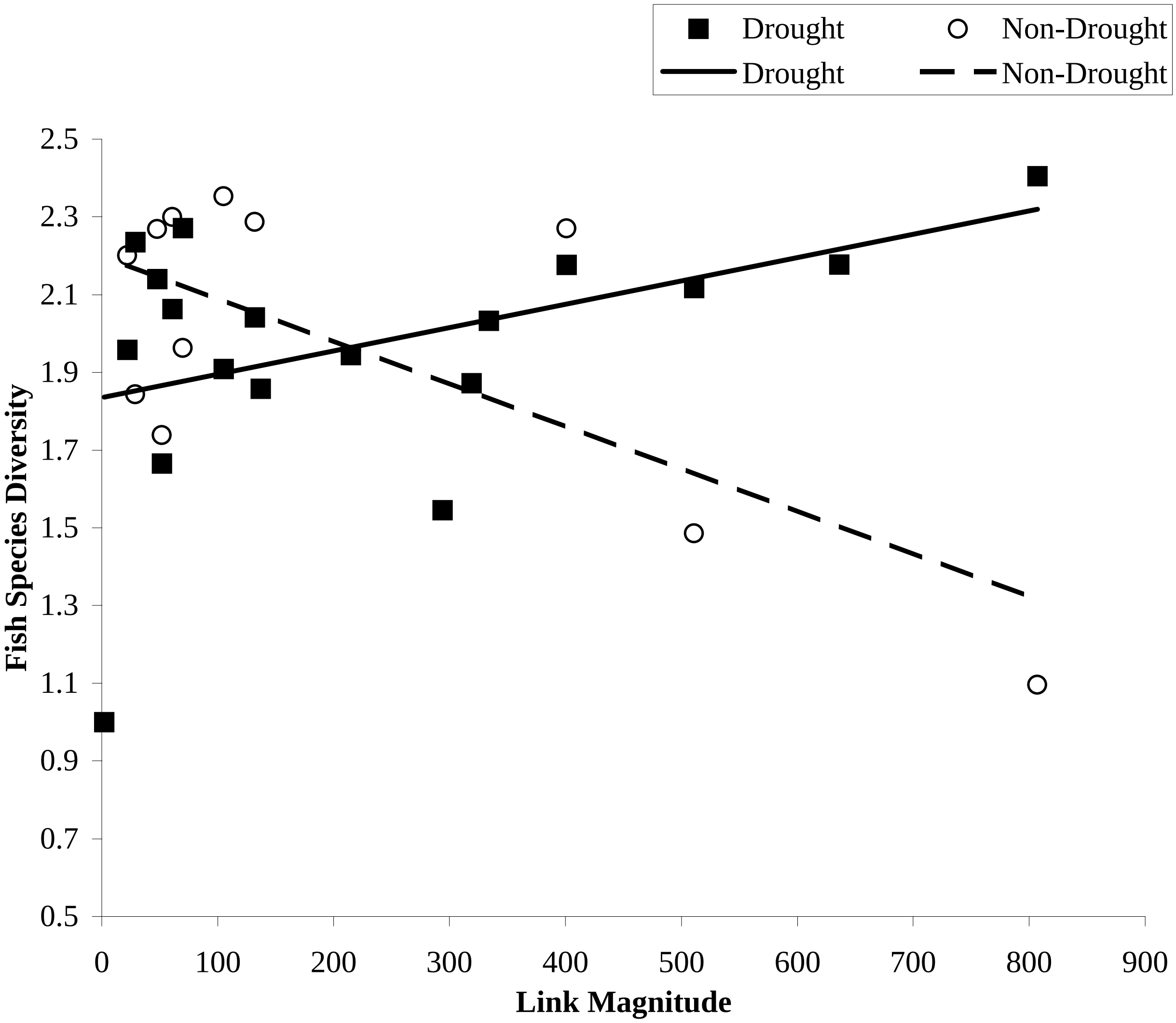

Figure 12. Relationship between drought, stream link magnitude, and fish species diversity in lower FRB streams during winter. Solid and dashed lines represent model predictions.

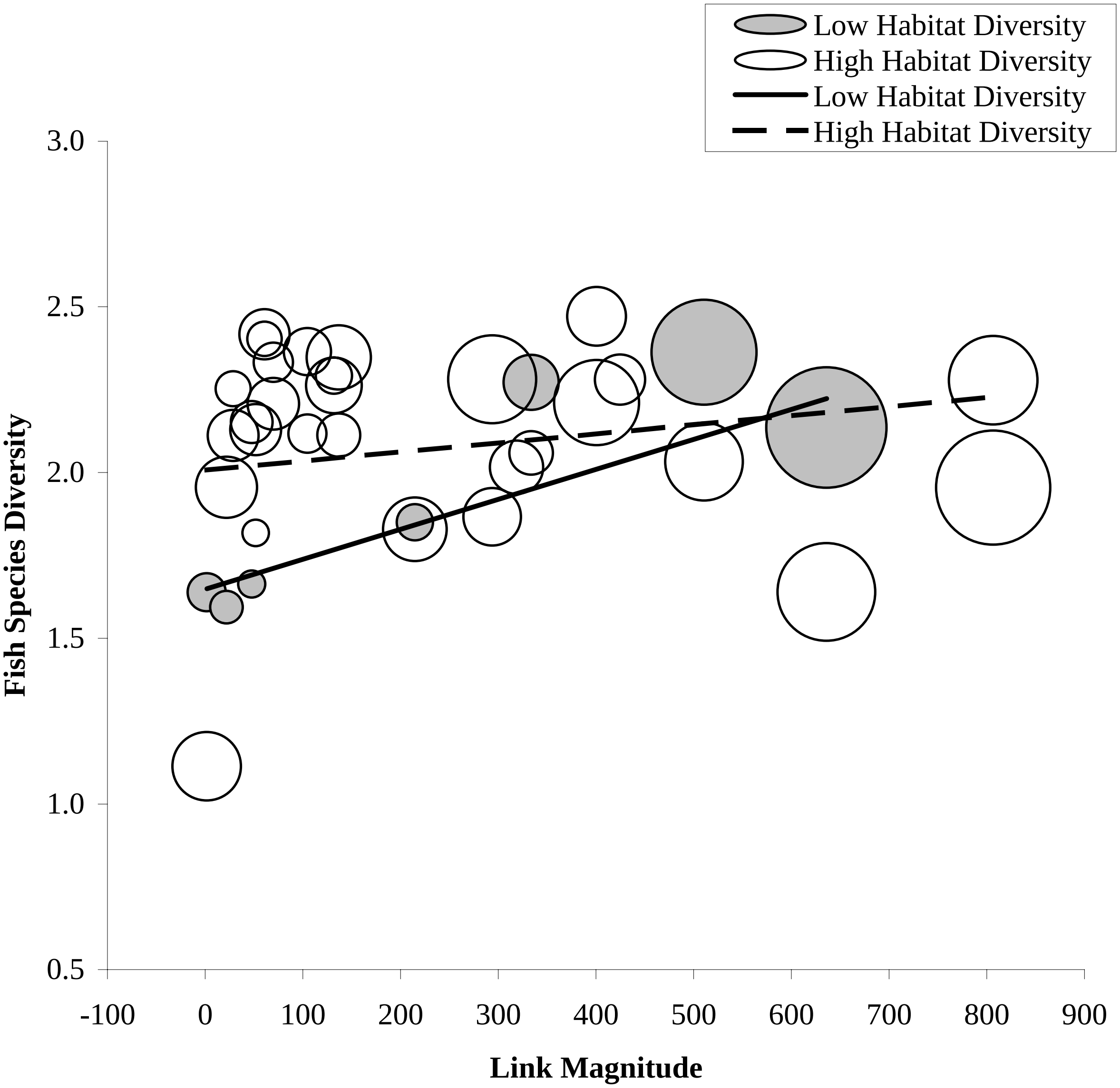

Figure 13. Relationship between stream link magnitude, habitat diversity, sample site area, and fish species diversity in lower FRB streams during spring. Shaded circles represent sample sites with low habitat diversity, and open circles represent sample sites with high habitat diversity. Sample site area is represented by circle size. Solid and dashed lines represent model predictions.

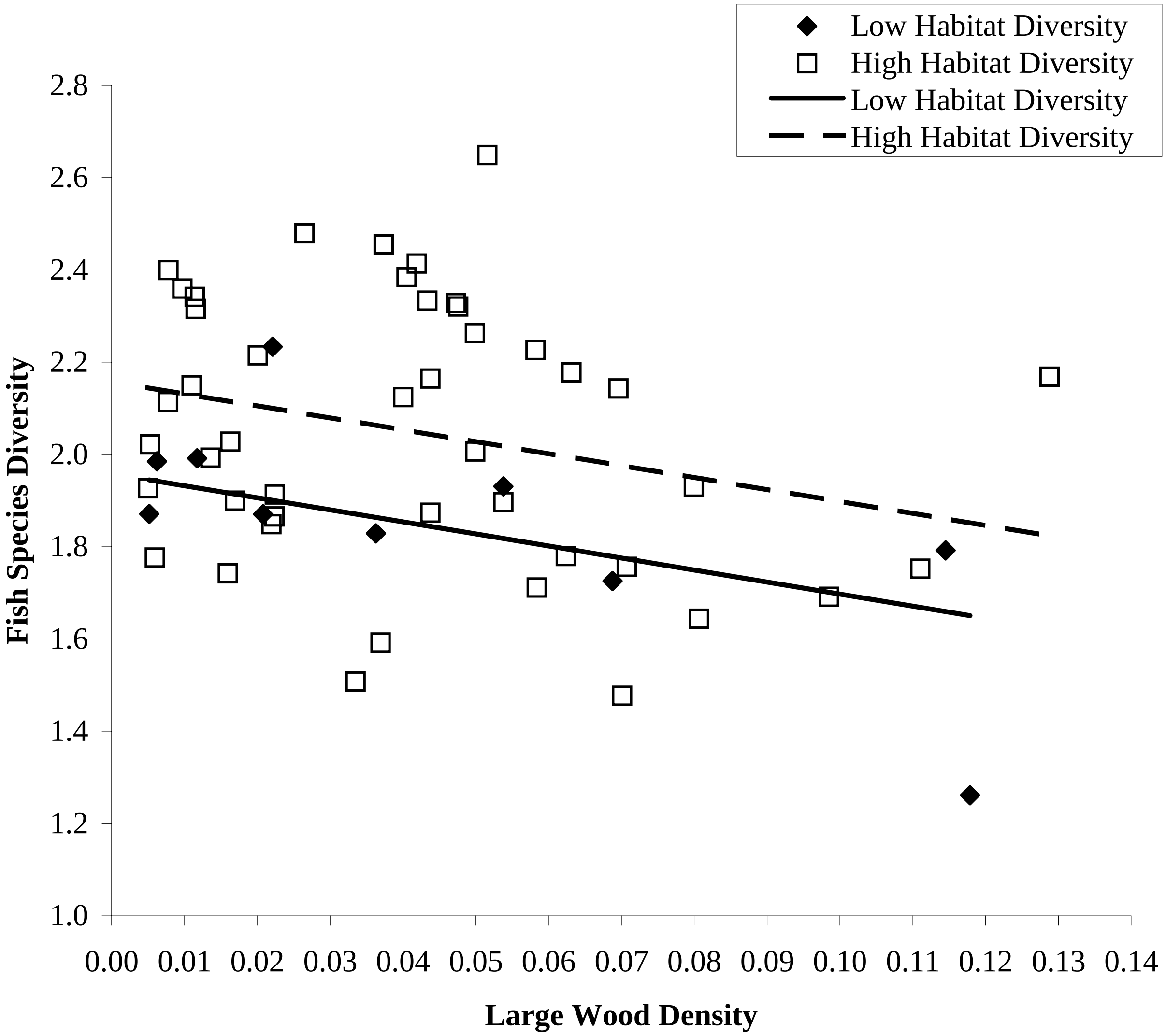

Figure 14. Relationship between habitat diversity, large wood density, and fish species diversity in lower FRB streams during summer. Solid and dashed lines represent model predictions.

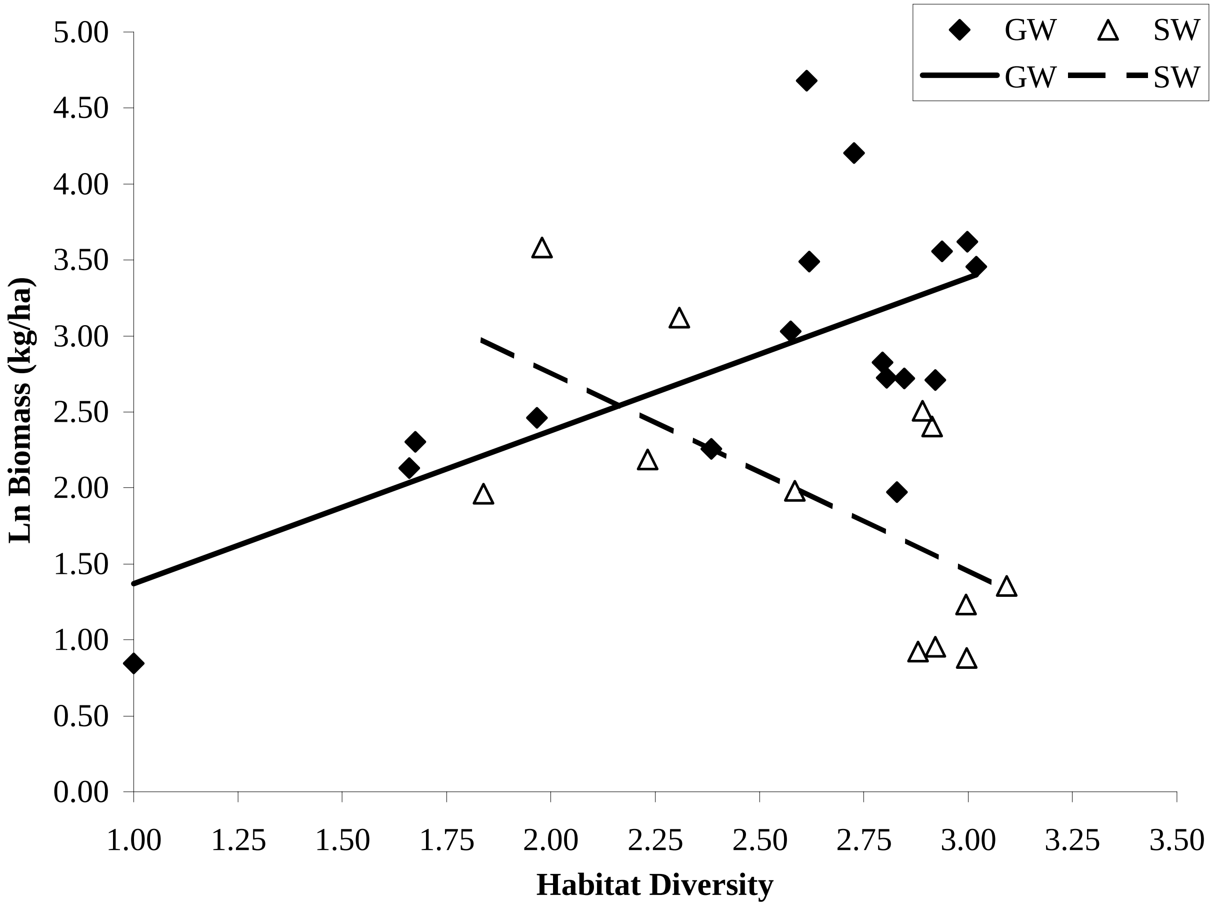

Figure 15. Relationship between groundwater, habitat diversity, and biomass in lower FRB streams during winter. GW indicates groundwater influenced sites, and SW indicates surface water dominated sites. Solid and dashed lines represent model predictions.

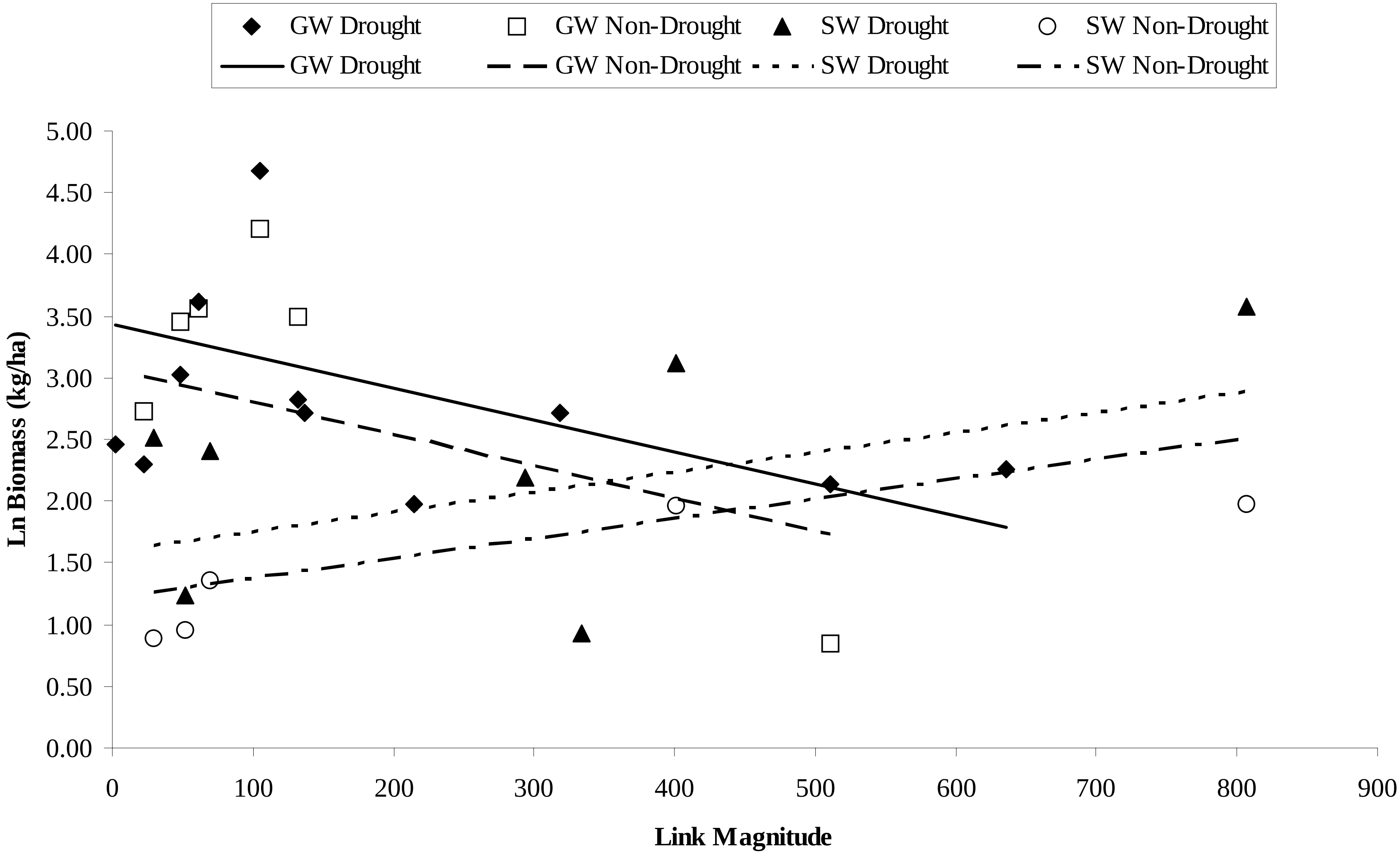

Figure 16. Relationship between drought, groundwater, link magnitude, and biomass in lower FRB streams during winter. GW indicates groundwater influenced sites, and SW indicates surface water dominated sites. Solid and dashed lines represent model predictions.

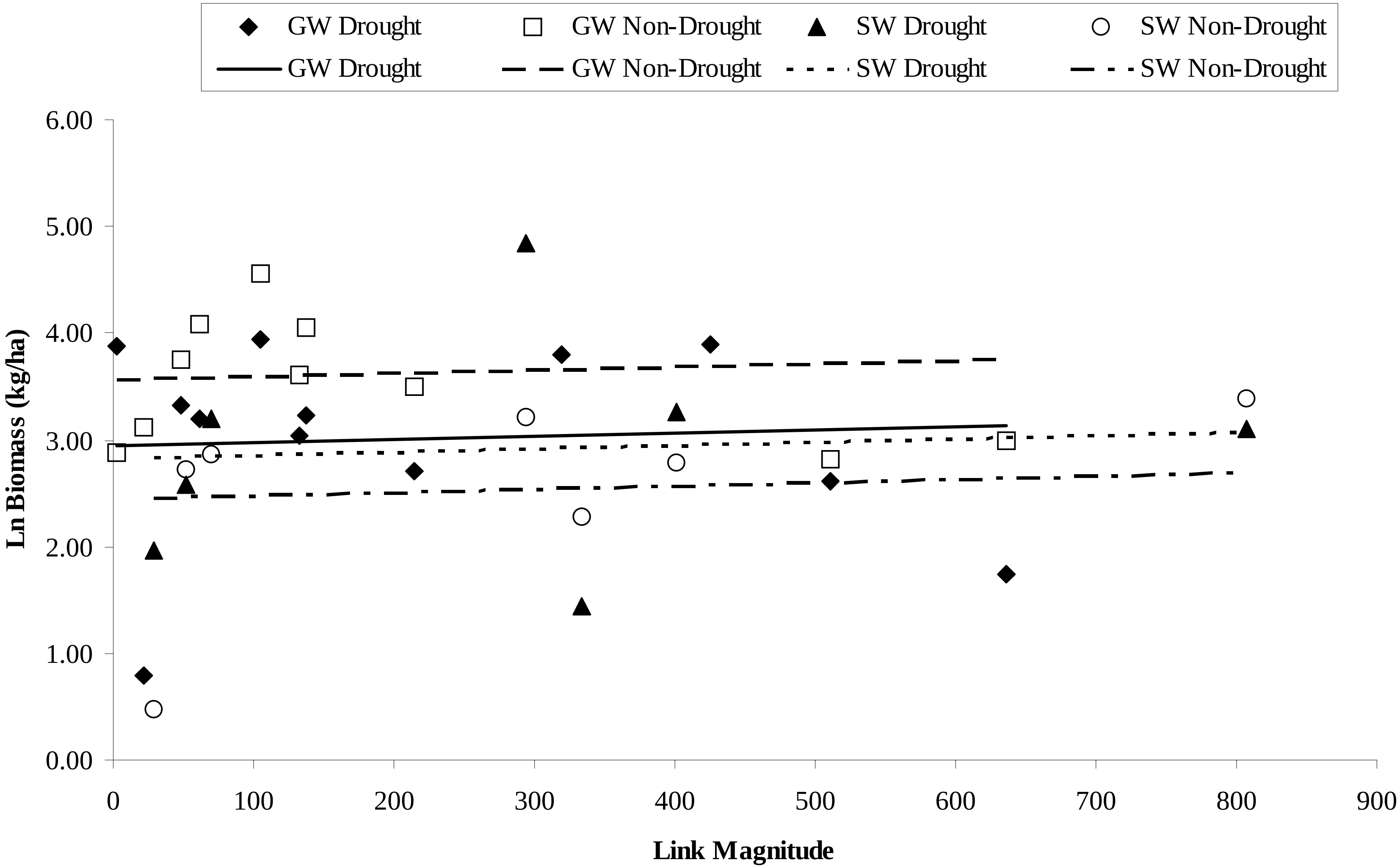

Figure 17. Relationship between link magnitude, groundwater, drought, and biomass in lower FRB streams during spring. GW indicates groundwater influenced sites, and SW indicates surface water dominated sites. Solid and dashed lines represent model predictions.

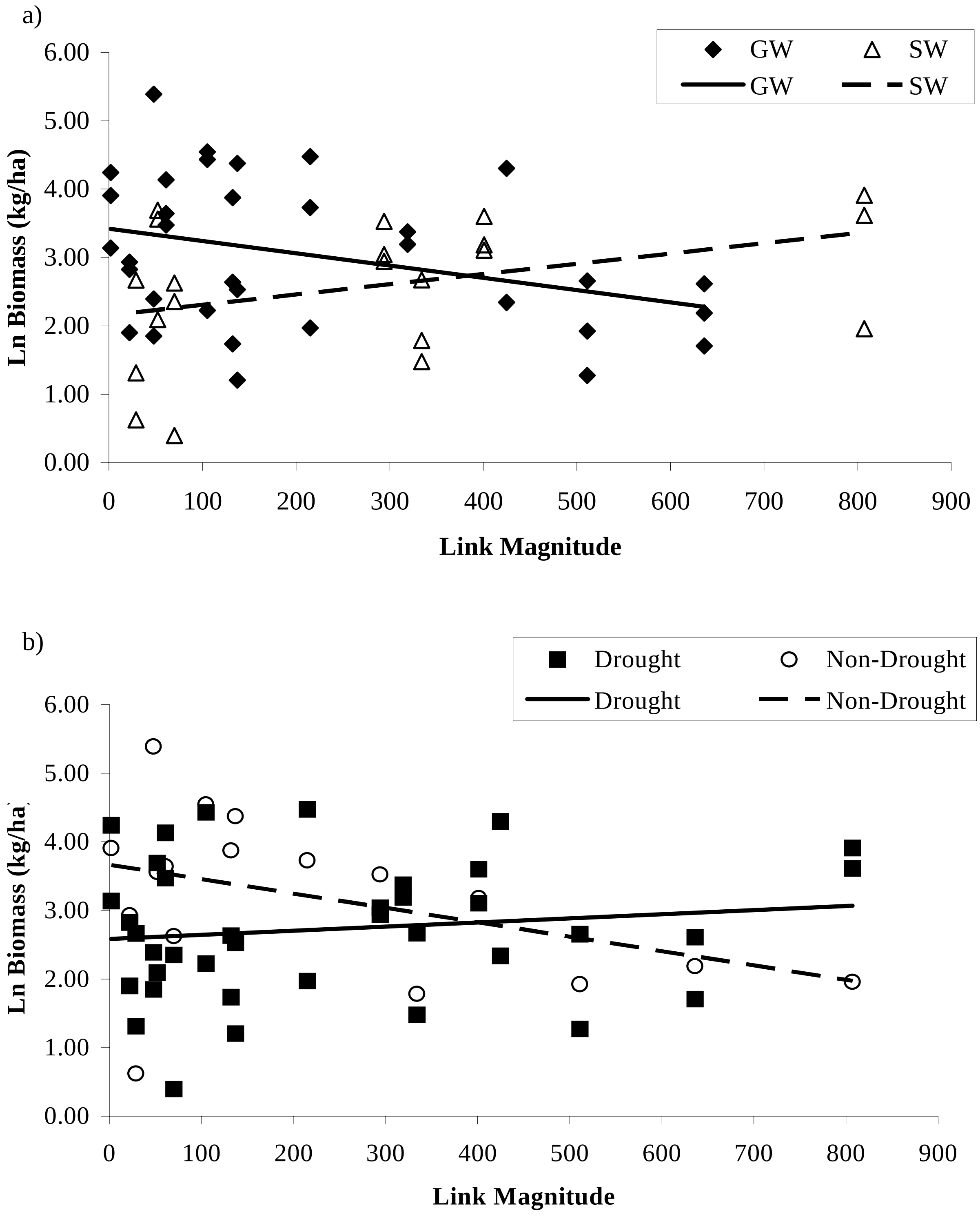

Figure 18. a) Relationship between stream link magnitude, groundwater, and biomass during summer, and b) relationship between stream link magnitude, drought, and biomass during summer in lower FRB streams. GW indicates groundwater influenced sites, and SW indicates surface water dominated sites. Solid and dashed lines represent model predictions.

APPENDIX A

Table A1. Samples where stream velocity was not measured because of equipment failure. Sample number, site code, and most strongly correlated USGS Stream gauge information is listed. See Table 1 for site code abbreviations.

Sample Number	Site	USGS Gauge Number	Gauge Location
80	CART	2353400	Pachitla Creek near Edison, GA
17 122	ICH3	2353500	Ichawaynochaway Creek at Milford, GA
121	KIN1	2350900	Kinchfoonee Creek near Dawson, GA
19 75	KIN2	2350600	Kinchfoonee Creek at Preston, GA

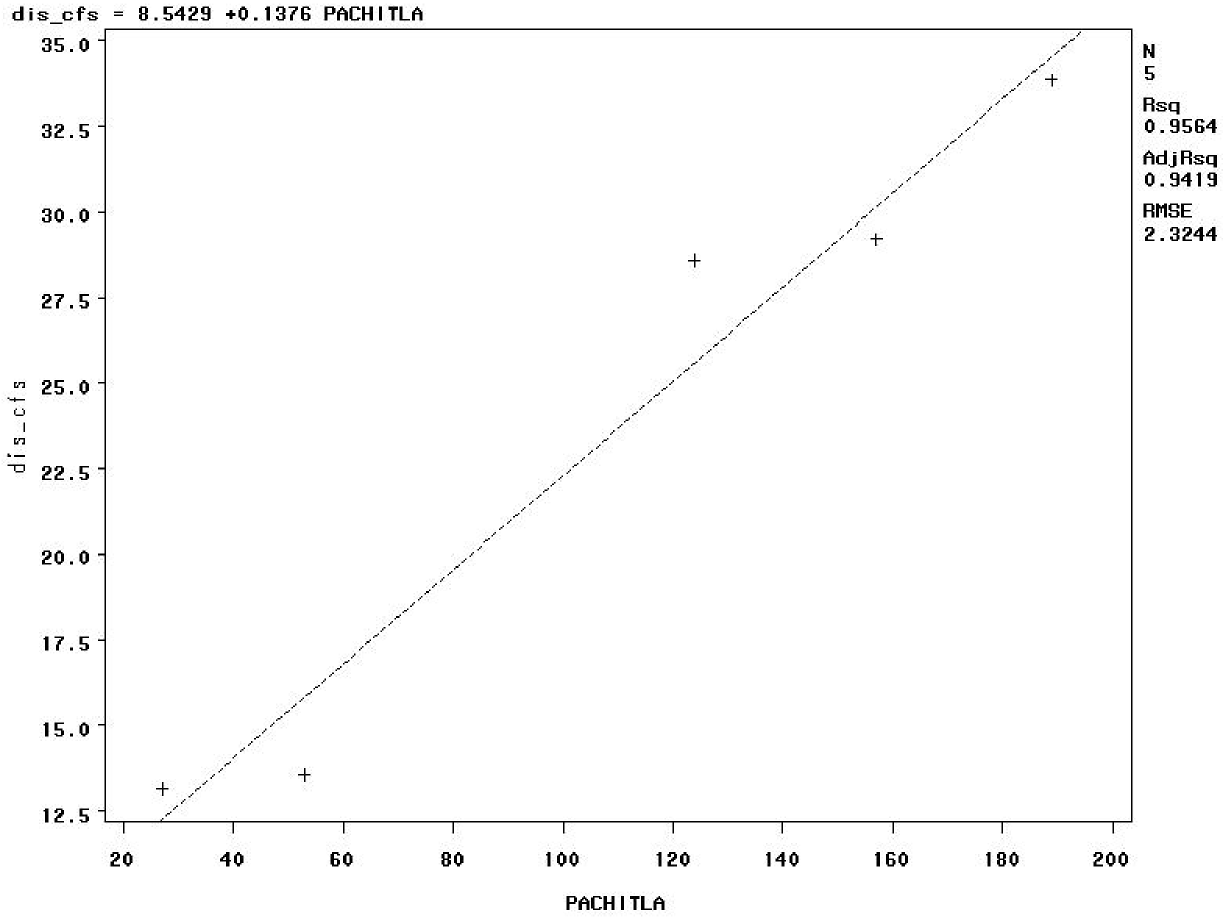

Figure A1. Regression model for estimating Carter Creek (CART) discharge with the most strongly correlated USGS gauging station. Discharge readings from USGS stream gauging station 2353400 on Pachitla Creek are on the abscissa, and discharge estimates from Carter Creek habitat samples are on the ordinate.

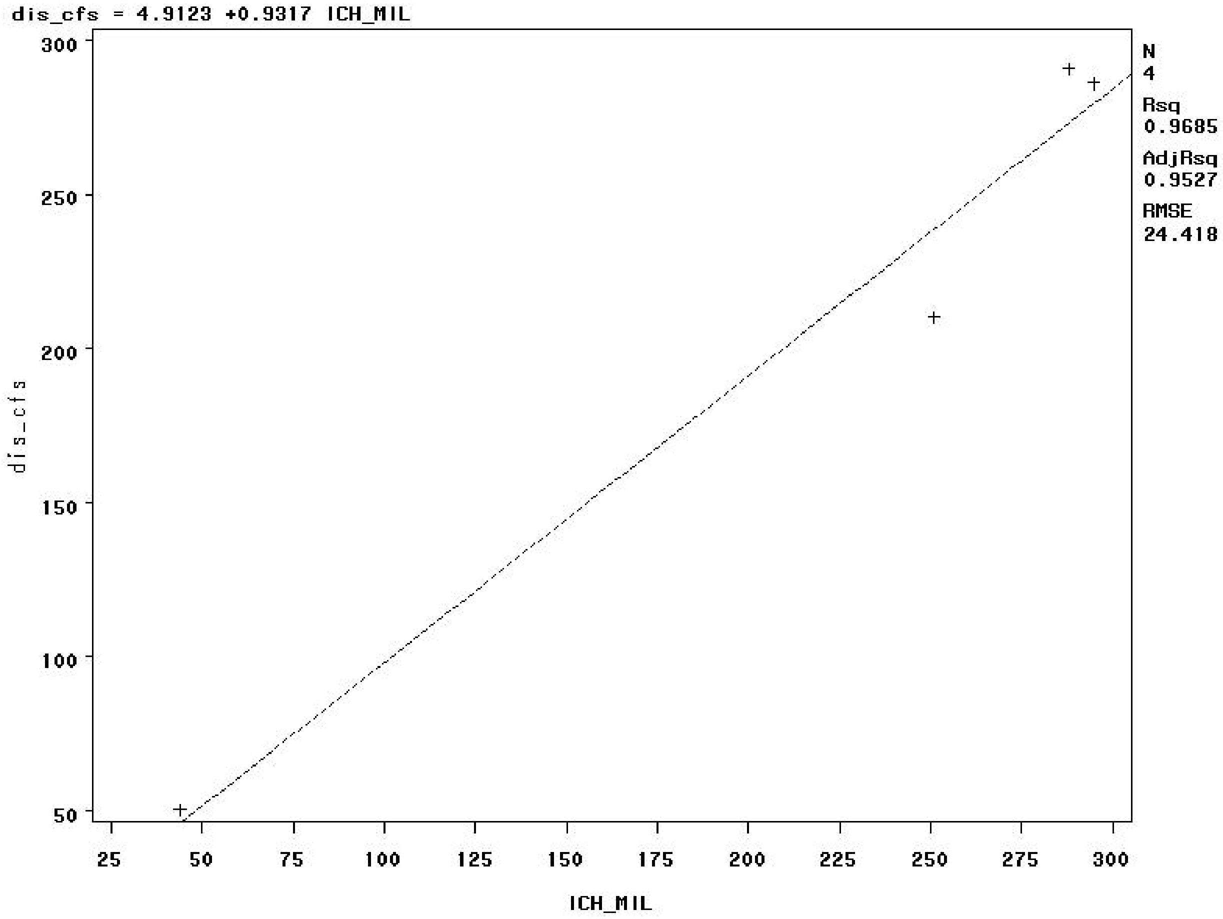

Figure A2. Regression model for estimating Ichawanochaway Creek (ICH3) discharge from the most correlated USGS gauging station. Discharge readings from USGS stream gauging station 2353500 on Ichawaynochaway Creek at Milford, GA are on the abscissa, and discharge estimates from Ichawaynochaway Creek habitat samples are on the ordinate.

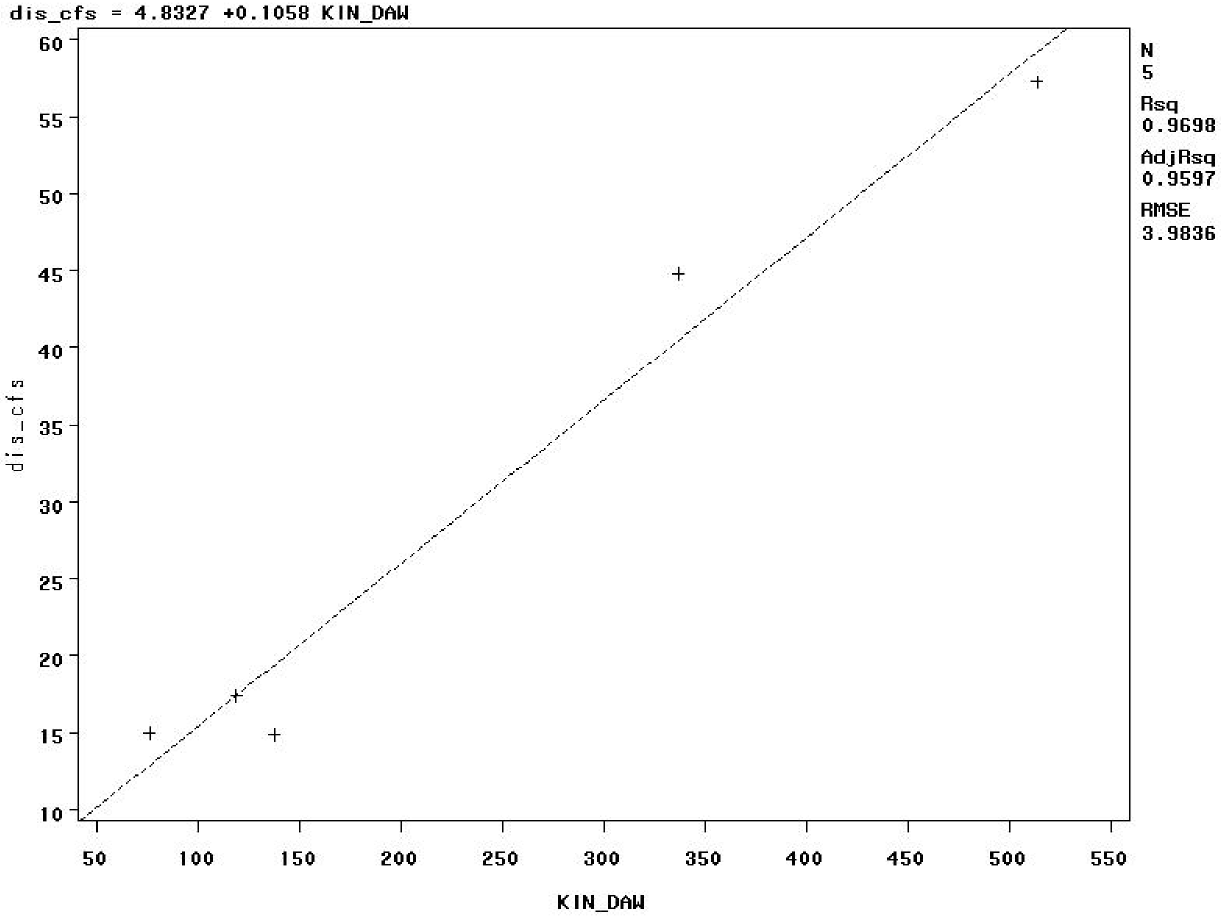

Figure A3. Regression model for estimating Kinchafoonee Creek (KIN1) discharge from the most correlated USGS gauging station. Discharge readings from USGS stream gauging station 2350900 on Kinchafoonee Creek near Dawson, GA are on the abscissa, and discharge estimates from Kinchafoonee Creek habitat samples are on the ordinate.

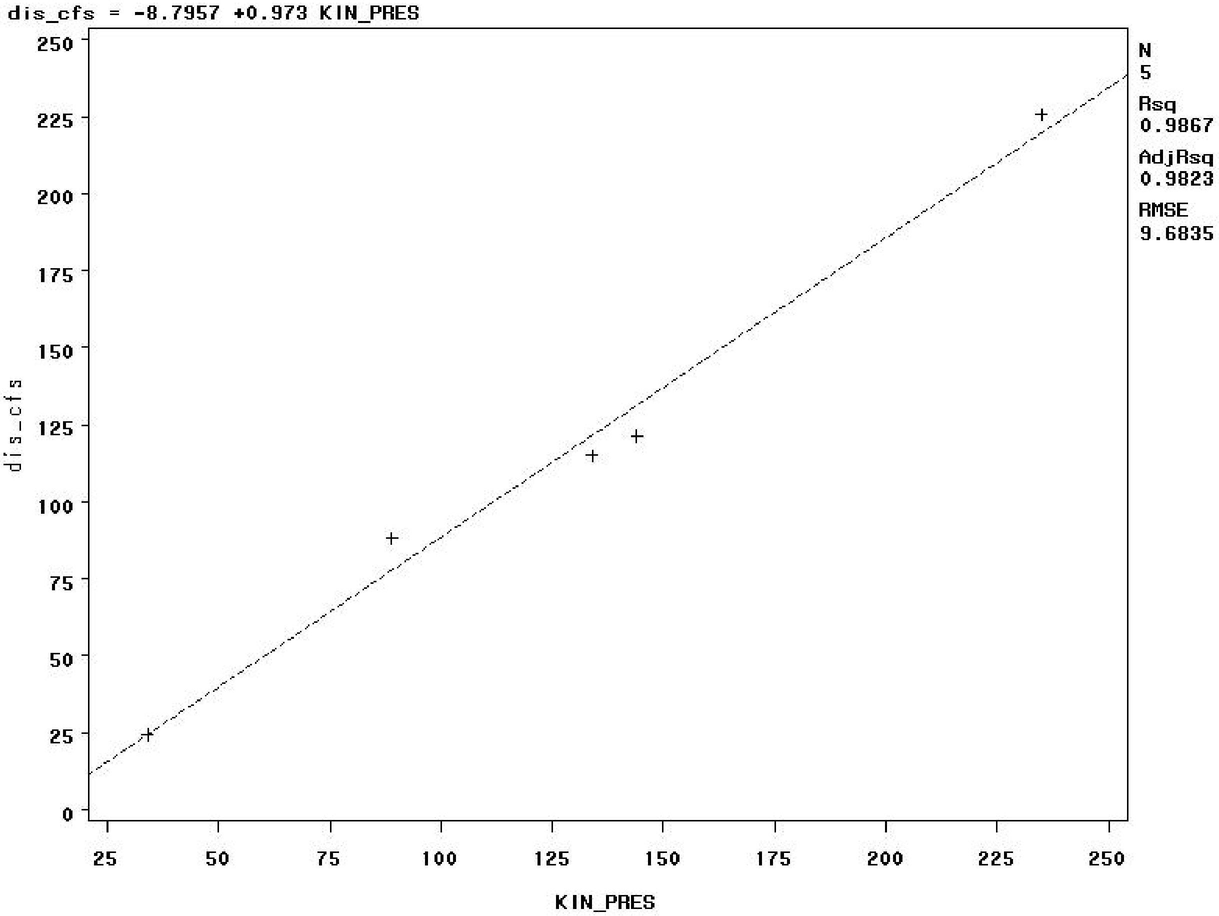

Figure A4. Regression model for estimating Kinchafoonee Creek (KIN2) discharge from the most correlated USGS gauging station. Discharge readings from USGS stream gauging station 2350600 on Kinchafoonee Creek at Preston, GA are on the abscissa, and discharge estimates from Kinchafoonee Creek habitat samples are on the ordinate.

APPENDIX B

Table B1. Species code, common name, scientific name, and family of fish species collected in lower FRB streams during 2001, 2002, and 2003.

Species Code	Common Name	Scientific Name	Family
AME	American Eel	*Anguilla rostrata*	Anguillidae
BPS	Banded Pigmy Sunfish	*Elassoma zonatum*	Elassomatidae
BFS	Bandfin Shiner	*Luxilus zonistius*	Cyprinidae
BBH	Black Bullhead	*Ameiurus melas*	Ictaluridae
BCR	Black Crappie	*Pomoxis nigromaculatus*	Centrarchidae
BRH	Black Redhorse	*Moxostoma duquesnei*	Catostomidae
BBD	Blackbanded Darter	*Percina nigrofasciata*	Percidae
BTS	Blacktail Shiner	*Cyprinella venusta*	Cyprinidae
BLG	Bluegill	*Lepomis macrochirus*	Centrarchidae
BOF	Bowfin	*Amia calva*	Amiidae
BRS	Brook Silverside	*Labidesthes sicculus*	Atherinidae
BRB	Brown Bullhead	*Ameriurus nebulosus*	Ictaluridae
BRD	Brown Darter	*Etheostoma edwini*	Percidae
CHP	Chain Pickerel	*Esox niger*	Esocidae
CCF	Channel Catfish	*Ichtalurus punctatus*	Ictaluridae
CLC	Clear Chub	*Hybopsis winchelli*	Cyprinidae
COS	Coastal Shiner	*Notropis petersoni*	Cyprinidae
CAR	Common carp	*Cyprinus carpio*	Cyprinidae
DOS	Dollar Sunfish	*Lepomis marginatus*	Centrarchidae
EST	Eastern Starhead Topminnow	*Fundulus escambiae*	Fundulidae
FHC	Flathead Catfish	*Pylodictus olivaris*	Ictaluridae
FLI	Flier	*Centrarchus macropterus*	Centrarchidae
GIS	Gizzard Shad	*Dorosoma cepedianum*	Clupeidae
GOS	Golden Shiner	*Notemigonus crysoleucas*	Cyprinidae
GOD	Goldstripe Darter	*Etheostoma parvipinne*	Percidae
GFR	Grayfin Redhorse	*Moxostoma grammarion*	Catostomidae
GJR	Greater Jumprock	*Moxostoma lachneri*	Catostomidae
GSF	Green Sunfish	*Lepomis cyanellus*	Centrarchidae
GUD	Gulf Darter	*Etheostoma swaini*	Percidae
HSS	Highscale Shiner	*Notropis hypsilepis*	Cyprinidae
ICS	Ironcolor Shiner	*Notropis chalybaeus*	Cyprinidae
LCS	Lake Chubsucker	*Erimyzon sucetta*	Catostomidae
LMB	Largemouth Bass	*Micropterus salmoides*	Centrarchidae
LNG	Longnose Gar	*Lepiosteus osseus*	Lepisosteidae
LNS	Longnose Shiner	*Notropis longirostris*	Cyprinidae
GAM	Mosquitofish	*Gambusia holbrooki*	Poeciliidae
PIP	Pirate Perch	*Aphredoderus sayanus*	Aphredoderidae
PNM	Pugnose Minnow	*Opsopoeodus emiliae*	Cyprinidae
RBS	Redbreast Sunfish	*Lepomis auritus*	Centrarchidae
RES	Redear Sunfish	*Lepomis microlophus*	Centrarchidae
REC	Redeye Chub	*Notropis harperi*	Cyprinidae
RFP	Redfin/Grass Pickerel	*Esox americanus x vermiculatus*	Esocidae
SFS	Sailfin Shiner	*Pteronotropis hypselopterus*	Cyprinidae
SDW	Shadow Bass	*Ambloplites ariommus*	Centrarchidae
SHB	Shoal Bass	*Micropterus cataractae*	Centrarchidae

Table B1. continued.

Species Code	Common Name	Scientific Name	Family
SJM	Silverjaw Minnow	*Ericymba buccata*	Cyprinidae
SBH	Snail Bullhead	*Ameiurus brunneus*	Ictaluridae
SBL	Southern Brook Lamprey	*Ichthyomyzon gagei*	Petromyzontidae
SMT	Speckeled Madtom	*Noturus leptacanthus*	Ictaluridae
SPB	Spotted Bullhead	*Ameiurus serracanthus*	Ictaluridae
SPG	Spotted Gar	*Lepiosteus oculatus*	Lepisosteidae
SPS	Spotted Sucker	*Minytrema melanops*	Catostomidae
SPT	Spotted Sunfish	*Lepomis punctatus*	Centrarchidae
MUL	Striped Mullet	*Mugil cephalus*	Mugilidae
SWD	Swamp Darter	*Etheostoma fusiforme*	Percidae
TPM	Tadpole Madtom	*Noturus gyrinus*	Ictaluridae
TLS	Taillight Shiner	*Notropis maculatus*	Cyprinidae
WAR	Warmouth	*Lepomis gulosus*	Centrarchidae
WES	Weed Shiner	*Notropis texanus*	Cyprinidae
YBH	Yellow Bullhead	*Ameirurus natalis*	Ictaluridae

Table B2. Species collected at each sample site in the lower FRB during 2001, 2002, and 2003. Species are indicated by codes that can be found in Table B1, and sample sites are indicated by abbreviations that can be found in Table1.

Species Code[a]	BEAR	CART	CHIC1	CHIC2	CHIC3	COOL1	COOL2	ICH1	ICH2	ICH3	KIN1	KIN2	KIN3	LIME	MILL	MUC1	MUC2	MUC3	SPR
BBD	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X
BBH									X							X			
BCR												X	X						
BFS							X												
BLG	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
BOF			X	X	X	X	X		X	X		X	X	X			X		
BPS			X	X	X	X	X	X									X		
BRB				X					X				X			X			X
BRD	X	X	X	X	X	X	X	X						X	X	X		X	
BRH													X						
BRS	X	X	X	X	X	X	X	X	X	X		X	X	X	X		X	X	X
BTS	X	X		X	X		X	X	X	X	X	X	X	X		X	X	X	X
CAR									X									X	
CCF							X		X			X	X	X	X		X	X	
CHP							X												
CLC	X	X	X	X	X		X	X	X		X	X	X	X	X	X	X	X	X
COS					X	X	X			X	X		X	X	X				X
DOS	X	X		X	X			X			X				X			X	
EST															X				
FHC							X		X	X					X				
FLI				X	X								X						
GAM		X	X	X	X	X	X	X					X	X	X	X		X	
GFR										X		X	X	X	X			X	
GIS															X				
GJR									X	X		X	X	X	X			X	
GOD			X	X						X									
GOS		X	X	X							X		X			X			
GSF				X	X	X	X						X	X	X			X	
GUD		X	X	X	X	X	X	X			X		X	X	X	X	X	X	X
HSS												X	X	X	X	X			

Table B2. continued.

Species Code[a]	BEAR	CART	CHIC1	CHIC2	CHIC3	COOL1	COOL2	ICH1	ICH2	ICH3	KIN1	KIN2	KIN3	LIME	MILL	MUC1	MUC2	MUC3	SPR
ICS		X	X	X	X	X	X		X		X			X	X			X	X
LCS												X			X				
LMB		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
LNG													X						
LNS	X	X				X		X	X		X	X	X		X	X	X	X	
MUL							X												
PIP	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
PNM	X	X	X					X	X		X	X	X	X	X	X	X	X	
RBS	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
REC	X		X	X	X	X	X		X					X				X	X
RES	X		X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X
RFP	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	
SBH	X															X	X	X	
SDW									X	X	X	X	X		X		X		
SFS	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
SHB									X	X			X						
SJM	X										X	X	X			X	X		
SMT	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X		X
SPB					X				X				X			X			
SPG				X									X		X				X
SPS	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
SPT	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
SWD	X	X	X	X	X	X	X	X		X		X		X	X	X	X		X
TLS		X																	
TPM																X			
WAR		X	X	X	X		X	X	X	X	X	X	X	X	X	X		X	X
WES	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
YBH			X	X	X	X		X	X		X	X	X	X		X			X

[a] American eel (*Anquilla rostrata*) and southern brook lamprey (*Ichthyomyzon gagei*) are not included in the table because they were excluded from analysis.

APPENDIX C

Table C1. Predictor variables, number of parameters (K), log-likelihood, AIC_c, ΔAIC_c, Akaike weights (*w*), and percent of maximum Akaike weight for the confidence set of candidate models (*i*) predicting natural log-transformed species richness in lower FRB streams during winter. Explanations of model parameters can be found in Table 4.

Candidate Model	K	Log Likelihood	AIC_c	ΔAIC_c	w_i	Percent of Maximum w_i
LK GW LK*GW AREA	7	17.02	-14.705	0.000	0.220	100.00
LK GW DT LK*GW	7	16.40	-13.470	1.235	0.119	53.93
LK GW DT	6	14.32	-12.815	1.890	0.086	38.87
LK GW LK*GW	6	13.99	-12.169	2.536	0.062	28.14
LK GW H_P LK*GW AREA	8	17.63	-12.066	2.639	0.059	26.73
LK GW AREA	6	13.83	-11.843	2.862	0.053	23.91
LK GW DT LK*GW AREA	8	17.38	-11.566	3.139	0.046	20.81
LK GW	5	11.94	-11.273	3.432	0.040	17.98

Table C2. Estimates of fixed and random effects for the selected best fitting hierarchical linear models for natural log-transformed species richness in lower FRB streams during winter.

Model:				90% Confidence Interval	
		Parameter estimate	Standard error	Lower	Upper
Link, Groundwater, Link*Groundwater, Sample site area:					
	Intercept	2.5650	0.0625	2.4550	2.6750
	Link	0.0007	0.0003	0.0002	0.0012
	Groundwater	0.2743	0.0759	0.1368	0.4119
	Link*Groundwater	-0.0006	0.0001	-0.0011	-0.0002
	Sample site area	0.1545	0.0613	0.0434	0.2655
	Random effect	<0.0001			
Link, Groundwater, Drought, Link*Groundwater:					
	Intercept	2.6893	0.0682	2.5693	2.8094
	Link	0.0013	0.0002	0.0010	0.0016
	Groundwater	0.2686	0.0775	0.1282	0.4090
	Drought	-0.1244	0.0563	-0.2264	-0.0223
	Link*Groundwater	-0.0005	0.0002	-0.0009	-0.0001
	Random effect	<0.0001			
Link, Groundwater, Drought:					
	Intercept	2.7488	0.0658	2.6335	2.8642
	Link	0.0011	0.0001	0.0008	0.0013
	Groundwater	0.1607	0.0604	0.0514	0.2701
	Drought	-0.1322	0.0600	-0.2410	-0.0234
	Random effect	<0.0001			
Link, Groundwater, Link*Groundwater:					
	Intercept	2.6181	0.0649	2.5038	2.7325
	Link	0.0013	0.0002	0.0010	0.0016
	Groundwater	0.2668	0.0837	0.1164	0.4171
	Link*Groundwater	-0.0005	0.0003	-0.0010	-0.0001
	Random effect	<0.0001			

Table C3. Predictor variables, number of parameters (K), log-likelihood, AIC_c, ΔAIC_c, Akaike weights (*w*), and percent of maximum Akaike weight for the confidence set of candidate models (*i*) predicting natural log-transformed species richness in lower FRB streams during spring. Explanations of model parameters can be found in Table 4.

Candidate Model	K	Log Likelihood	AIC_c	ΔAIC_c	w_i	Percent of Maximum w_i
LK DT	5	5.73	0.540	0.000	0.178	100.00
LK DT LWD	6	6.45	1.995	1.455	0.086	48.32
LK GW DT	6	6.44	2.025	1.485	0.084	47.59
LK DT AREA	6	6.11	2.679	2.139	0.061	34.31
LK GW DT LK*GW	7	7.47	3.067	2.527	0.050	28.27
LK DT H_P	6	5.89	3.119	2.579	0.049	27.54
LK DT LK*DT	6	5.83	3.228	2.688	0.046	26.08
LK AREA	5	4.36	3.274	2.733	0.045	25.49
LK GW DT LWD	7	6.91	4.178	3.638	0.029	16.22
LK GW DT GW*DT	7	6.86	4.286	3.746	0.027	15.37
LK DT LWD AREA	7	6.72	4.551	4.011	0.024	13.46
LK LWD AREA	6	5.14	4.614	4.074	0.023	13.04
LK GW DT AREA	7	6.68	4.649	4.109	0.023	12.82
LK DT H_P LWD	7	6.62	4.758	4.218	0.022	12.13
LK GW DT LK*DT	7	6.56	4.888	4.348	0.020	11.37
LK GW DT H_P	7	6.56	4.889	4.349	0.020	11.37
LK GW LK*GW AREA	7	6.55	4.902	4.362	0.020	11.29

Table C4. Estimates of fixed and random effects for the selected best fitting hierarchical linear models for natural log-transformed species richness in lower FRB streams during spring.

Model:				90% Confidence Interval	
		Parameter estimate	Standard error	Lower	Upper
Link, Drought:					
	Intercept	2.9645	0.0630	2.8549	3.0741
	Link	0.0009	0.0002	0.0006	0.0012
	Drought	-0.2339	0.0716	-0.3589	-0.1089
	Random effect	<0.0001			
Link, Drought, Large wood density:					
	Intercept	3.0316	0.0857	2.8824	3.1807
	Link	0.0008	0.0002	0.0005	0.0011
	Drought	-0.2084	0.0739	-0.3379	-0.0790
	Large wood density	-1.5194	1.3444	-3.8762	0.8374
	Random effect	<0.0001			
Link, Groundwater, Drought:					
	Intercept	2.9096	0.0791	2.7714	3.0477
	Link	0.0009	0.0002	0.0007	0.0012
	Groundwater	0.0817	0.0732	-0.0461	0.2095
	Drought	-0.2379	0.0705	-0.3609	-0.1149
	Random effect	<0.0001			
Link, Drought, Sample site area:					
	Intercept	2.9178	0.0877	2.7652	3.0705
	Link	0.0007	0.0003	0.0001	0.0013
	Drought	-0.1825	0.0981	-0.3546	-0.0105
	Sample site area	0.0562	0.0742	-0.0738	0.1862
	Random effect	<0.0001			

Table C5. Predictor variables, number of parameters (K), log-likelihood, AIC_c, ΔAIC_c, Akaike weights (*w*), and percent of maximum Akaike weight for the confidence set of candidate models (*i*) predicting natural log-transformed species richness in lower FRB streams during summer. Explanations of model parameters can be found in Table 4.

Candidate Model	K	Log Likelihood	AIC_c	ΔAIC_c	w_i	Percent of Maximum w_i
LK DT	5	-8.38	27.990	0.000	0.114	100.00
LK DT AREA	6	-7.37	28.491	0.501	0.089	77.84
LK DT H_P DT*H_P AREA	8	-4.82	28.770	0.780	0.077	67.71
LK DT LK*DT AREA	7	-6.39	29.164	1.175	0.063	55.58
LK DT H_P DT*H_P	7	-6.78	29.935	1.945	0.043	37.81
LK DT H_P AREA	7	-6.85	30.093	2.103	0.040	34.94
LK DT LWD	6	-8.19	30.124	2.135	0.039	34.40
LK DT LK*DT	6	-8.19	30.130	2.141	0.039	34.29
LK AREA	5	-9.46	30.144	2.154	0.039	34.06
LK H_P AREA	6	-8.23	30.203	2.213	0.038	33.07
LK GW DT	6	-8.29	30.336	2.346	0.035	30.94
LK GW DT LK*GW AREA	8	-5.84	30.806	2.816	0.028	24.46
LK DT LWD AREA	7	-7.29	30.957	2.968	0.026	22.68
LK GW DT AREA	7	-7.31	31.012	3.022	0.025	22.07
LK GW DT LK*GW	7	-7.44	31.265	3.275	0.022	19.45
LK GW LK*GW AREA	7	-7.51	31.400	3.411	0.021	18.17
LK DT H_P LK*DT AREA	8	-6.34	31.809	3.820	0.017	14.81
LK GW DT LK*DT AREA	8	-6.39	31.905	3.915	0.016	14.12
LK GW H_P LK*GW AREA	8	-6.42	31.977	3.987	0.016	13.62
LK H_P LK*H_P AREA	7	-7.94	32.256	4.266	0.013	11.85
LK DT H_P LWD	7	-7.95	32.287	4.297	0.013	11.66
LK GW DT GW*DT	7	-8.01	32.402	4.412	0.013	11.01
LK LWD AREA	6	-9.33	32.410	4.421	0.012	10.97
LK DT H_P	6	-9.39	32.523	4.533	0.012	10.37
LK GW AREA	6	-9.40	32.541	4.552	0.012	10.27

Table C6. Estimates of fixed and random effects for the selected best fitting hierarchical linear models for natural log-transformed species richness in lower FRB streams during summer.

Model:				90% Confidence Interval	
		Parameter estimate	Standard error	Lower	Upper
Link, Drought:					
	Intercept	3.0062	0.0800	2.8670	3.1453
	Link	0.0008	0.0002	0.0005	0.0011
	Drought	-0.2504	0.0841	-0.3925	-0.1083
	Random effect	<0.0001			
Link, Drought, Sample site area:					
	Intercept	2.9311	0.0952	2.7655	3.0967
	Link	0.0004	0.0003	-0.0001	0.0010
	Drought	-0.1911	0.0929	-0.3481	-0.0340
	Sample site area	0.0972	0.0695	-0.0203	0.2147
	Random effect	<0.0001			
Link, Drought, Habitat diversity, Drought*Habitat Diversity, Sample site area:					
	Intercept	1.6093	0.5928	0.5780	2.6405
	Link	0.0004	0.0003	-0.0001	0.0010
	Drought	1.0878	0.6234	0.0319	2.1438
	Habitat diversity	0.4665	0.2067	0.1163	0.8166
	Drought*Habitat diversity	-0.4671	0.2306	-0.8578	-0.0764
	Sample site area	0.1369	0.0691	0.0200	0.2539
	Random effect	<0.0001			
Link, Drought, Link*Drought, Sample site area:					
	Intercept	3.0215	0.1007	2.8463	3.1968
	Link	-0.0002	0.0004	-0.0010	0.0005
	Drought	-0.3477	0.1144	-0.5413	-0.1542
	Link*Drought	0.0008	0.0004	0.0002	0.0014
	Sample site area	0.1333	0.0691	0.0163	0.2503
	Random effect	0.0009	0.0100	-0.0155	0.0173
Link, Drought, Habitat diversity, Drought*Habitat diversity:					
	Intercept	1.9979	0.5791	0.9905	3.0054
	Link	0.0010	0.0002	0.0006	0.0013
	Drought	0.7707	0.6237	-0.2848	1.8262
	Habitat diversity	0.3638	0.2071	0.0133	0.7144
	Drought*Habitat diversity	-0.3819	0.2346	-0.7789	0.0151
	Random effect	<0.0001			

Table C6. continued.

Model:

	Parameter estimate	Standard error	90% Confidence Interval Lower	Upper
Link, Drought, Habitat diversity, Sample site area:				
Intercept	2.6953	0.2619	2.2396	3.1510
Link	0.0004	0.0003	-0.0002	0.0009
Drought	-0.1602	0.0975	-0.3252	0.0048
Habitat diversity	0.0835	0.0865	-0.0629	0.2298
Sample site area	0.1109	0.0703	-0.0081	0.2299
Random effect	<0.0001			

Table C7. Predictor variables, number of parameters (K), log-likelihood, AIC_c, ΔAIC_c, Akaike weights (*w*), and percent of maximum Akaike weight for the confidence set of candidate models (*i*) for predicting fish species diversity in lower FRB streams during winter. Explanations of model parameters can be found in Table 4.

Candidate Model	K	Log Likelihood	AIC_c	ΔAIC_c	w_i	Percent of Maximum w_i
LK DT LK*DT	6	-4.01	23.844	0.000	0.292	100.00
LK GW DT LK*DT AREA	8	-1.54	26.290	2.446	0.086	29.44
LK DT LK*DT AREA	7	-3.65	26.635	2.791	0.072	24.77
LK	4	-8.58	26.821	2.977	0.066	22.57
LK DT H_P LK*DT	7	-3.89	27.113	3.269	0.057	19.50
LK GW DT LK*DT	7	-3.96	27.246	3.402	0.053	18.25
LK AREA	5	-7.59	27.782	3.938	0.041	13.96
LK H_P LK*H_P	6	-6.17	28.149	4.305	0.034	11.62
LK H_P	5	-7.92	28.442	4.598	0.029	10.04

Table C8. Estimates of fixed and random effects for the selected best fitting hierarchical linear models for fish species diversity in lower FRB streams during winter.

Model:			90% Confidence Interval	
	Parameter estimate	Standard error	Lower	Upper
Link, Drought, Link*Drought:				
Intercept	2.2014	0.1089	2.0112	2.3915
Link	-0.0011	0.0003	-0.0018	-0.0005
Drought	-0.3663	0.1391	-0.6213	-0.1114
Link*Drought	0.0017	0.0004	0.0009	0.0025
Random effect	0.0060	0.0443	-0.0666	0.0785
Link, Groundwater, Drought, Link*Drought, Sample site area:				
Intercept	2.2756	0.1542	2.0052	2.5459
Link	-0.0003	0.0009	-0.0020	0.0015
Groundwater	0.0641	0.1086	-0.1379	0.2660
Drought	-0.4530	0.1587	-0.7481	-0.1578
Link*Drought	0.0015	0.0005	0.0006	0.0024
Sample site area	-0.1777	0.1801	-0.5126	0.1573
Random effect	<0.0001			
Link, Drought, Link*Drought, Sample site area:				
Intercept	2.3000	0.1481	2.0414	2.5586
Link	-0.0004	0.0009	-0.0021	0.0013
Drought	-0.4370	0.1573	-0.7295	-0.1445
Link*Drought	0.0015	0.0005	0.0006	0.0024
Sample site area	-0.1522	0.1763	-0.4801	0.1757
Random effect	0.0011	0.0414	-0.0668	0.0690

Table C9. Predictor variables, number of parameters (K), log-likelihood, AIC$_c$, ΔAIC$_c$, Akaike weights (*w*), and percent of maximum Akaike weight for the confidence set of candidate models (*i*) for predicting fish species diversity in lower FRB streams during spring. Explanations of model parameters can be found in Table 4.

Candidate Model	K	Log Likelihood	AIC$_c$	ΔAIC$_c$	w_i	Percent of Maximum w_i
LK H_P LK*H_P AREA	7	1.13	15.737	0.000	0.207	100.00
LK H_P LK*H_P	6	-1.27	17.440	1.703	0.088	42.69
LK	4	-4.12	17.525	1.788	0.085	40.90
LK GW H_P LK*H_P AREA	8	1.64	18.045	2.308	0.065	31.54
LK DT	5	-3.26	18.517	2.780	0.051	24.90
LK DT AREA	6	-1.83	18.558	2.821	0.050	24.40
LK GW	5	-3.57	19.150	3.412	0.038	18.16
LK GW H_P LK*H_P	7	-0.66	19.324	3.586	0.034	16.64
LK DT LWD	6	-2.43	19.761	4.023	0.028	13.38
LK LWD	5	-3.93	19.861	4.123	0.026	12.72
LK DT LWD AREA	7	-1.05	20.104	4.367	0.023	11.27
LK H_P	5	-4.07	20.133	4.395	0.023	11.11
LK AREA	5	-4.12	20.234	4.496	0.022	10.56

Table C10. Estimates of fixed and random effects for the selected best fitting hierarchical linear models for fish species diversity in lower FRB streams during spring.

Model:			90% Confidence Interval	
	Parameter estimate	Standard error	Lower	Upper
Link, Habitat diversity, Link*Habitat diversity, Sample site area:				
Intercept	0.6990	0.3782	0.0410	1.3569
Link	0.0047	0.0012	0.0026	0.0069
Habitat diversity	0.5406	0.1457	0.2840	0.7971
Link*Habitat diversity	-0.0015	0.0004	-0.0022	-0.0008
Sample site area	-0.1855	0.0765	-0.3202	-0.0507
Random effect	0.0025	0.0189	-0.0285	0.0334
Link, Habitat diversity, Link*Habitat diversity:				
Intercept	1.1345	0.3844	0.4658	1.8033
Link	0.0024	0.0009	0.0008	0.0039
Habitat diversity	0.3463	0.1446	0.0928	0.5998
Link*Habitat diversity	-0.0009	0.0003	-0.0015	-0.0002
Random effect	0.0199	0.0214	-0.0152	0.0549

Table C11. Predictor variables, number of parameters (K), log-likelihood, AIC_c, ΔAIC_c, Akaike weights (*w*), and percent of maximum Akaike weight for the confidence set of candidate models (*i*) predicting fish species diversity in lower FRB streams during summer. See Table 4 for model parameter explanations.

Candidate Model	K	Log Likelihood	AIC_c	ΔAIC_c	w_i	Percent of Maximum w_i
LK H_P LWD	6	-1.57	16.900	0.000	0.247	100.00
LK H_P	5	-3.46	18.148	1.248	0.132	53.58
LK GW H_P LWD	7	-1.35	19.092	2.192	0.083	33.42
LK DT H_P LWD	7	-1.43	19.240	2.340	0.077	31.04
LK H_P LWD AREA	7	-1.43	19.245	2.346	0.076	30.95
LK H_P AREA	6	-3.40	20.545	3.645	0.040	16.16
LK GW H_P	6	-3.40	20.555	3.655	0.040	16.08
LK H_P LK*H_P	6	-3.40	20.557	3.658	0.040	16.06
LK DT H_P LWD AREA	8	-1.12	21.372	4.473	0.026	10.69

Table C12. Estimates of fixed and random effects for the selected best fitting hierarchical linear models for fish species diversity in lower FRB streams during summer.

Model:			90% Confidence Interval	
	Parameter estimate	Standard error	Lower	Upper
Link, Habitat diversity, Large wood density:				
Intercept	1.6282	0.2204	1.2448	2.0116
Link	<0.0001	0.0002	-0.0003	0.0003
Habitat diversity	0.1972	0.0747	0.0708	0.3235
Large wood density	-2.6080	1.3383	-4.8709	-0.3451
Random effect	<0.0001			
Link, Habitat diversity:				
Intercept	1.4204	0.1994	1.0735	1.7673
Link	0.0002	0.0002	-0.0001	0.0005
Habitat diversity	0.2169	0.0766	0.0875	0.3463
Random effect	<0.0001			

Table C13. Predictor variables, number of parameters (K), log-likelihood, AIC$_c$, ΔAIC$_c$, Akaike weights (*w*), and percent of maximum Akaike weight for the confidence set of candidate models (*i*) predicting biomass in lower FRB streams during winter. See Table 4 for model parameter explanations.

Candidate Model	K	Log Likelihood	AIC$_c$	ΔAIC$_c$	w_i	Percent of Maximum w_i
LK GW H_P GW*H_P	7	-28.68	76.692	0.000	0.552	100.00
LK GW LK*GW	6	-31.69	79.190	2.499	0.158	28.67
LK GW DT LK*GW	7	-30.69	80.722	4.030	0.074	13.33
LK GW DT GW*DT	7	-30.79	80.910	4.218	0.067	12.13
LK GW H_P LK*GW	7	-30.86	81.060	4.369	0.062	11.25

Table C14. Estimates of fixed and random effects for the selected best fitting hierarchical linear models for biomass in lower FRB streams during winter.

Model:			90% Confidence Interval	
	Parameter estimate	Standard error	Lower	Upper
Link, Groundwater, Habitat diversity, Groundwater*Habitat diversity:				
Intercept	6.1356	1.5764	3.3720	8.8992
Link	-0.0005	0.0007	-0.0018	0.0007
Groundwater	-5.4867	1.5637	-8.3532	-2.6201
Habitat diversity	-1.5443	0.5514	-2.5550	-0.5336
Groundwater*Habitat diversity	2.4724	0.5818	1.4059	3.5390
Random effect	0.0476	0.1310	-0.1672	0.2623
Link, Groundwater, Link*Groundwater:				
Intercept	1.4512	0.3167	0.8935	2.0090
Link	0.0017	0.0008	0.0002	0.0031
Groundwater	1.8741	0.4065	1.1440	2.6041
Link*Groundwater	-0.0042	0.0013	-0.0064	-0.0019
Random effect	0.0734	0.1542	-0.1796	0.3263
Link, Groundwater, Drought, Link*Groundwater:				
Intercept	1.2197	0.3624	0.5813	1.8581
Link	0.0016	0.0009	0.0001	0.0032
Groundwater	1.8418	0.4278	1.0663	2.6172
Drought	0.3754	0.2328	-0.0466	0.7974
Link*Groundwater	-0.0042	0.0013	-0.0065	-0.0018
Random effect	0.1695	0.1647	-0.1006	0.4395
Link, Groundwater, Drought, Groundwater*Drought:				
Intercept	1.2675	0.4053	0.5571	1.9780
Link	-0.0010	0.0008	-0.0017	0.0013
Groundwater	1.5880	0.4473	0.7680	2.4081
Drought	1.0670	0.2583	0.5934	1.5405
Groundwater*Drought	-1.0920	0.3480	-1.7299	-0.4540
Random effect	0.4853	0.2035	0.1515	0.8191
Link, Groundwater, Habitat diversity, Link*Groundwater:				
Intercept	0.2603	0.9486	-1.4104	1.9310
Link	0.0021	0.0008	0.0006	0.0036
Groundwater	1.9642	0.3876	1.2616	2.6668
Habitat diversity	0.4078	0.3074	-0.1494	0.9650
Link*Groundwater	-0.0041	0.0012	-0.0063	-0.0020
Random effect	0.0329	0.1507	-0.2143	0.2800

Table C15. Predictor variables, number of parameters (K), log-likelihood, AIC$_c$, ΔAIC$_c$, Akaike weights (*w*), and percent of maximum Akaike weight for the confidence set of candidate models (*i*) predicting biomass in lower FRB streams during spring. See Table 4 for model parameter explanations.

Candidate Model	K	Log Likelihood	AIC$_c$	ΔAIC$_c$	w_i	Percent of Maximum w_i
LK	4	-46.41	102.116	0.000	0.137	100.00
LK GW DT GW*DT	7	-42.20	102.392	0.277	0.119	87.08
LK GW	5	-45.21	102.413	0.297	0.118	86.20
LK GW LK*GW	6	-43.98	102.864	0.749	0.094	68.77
LK DT	5	-46.07	104.147	2.031	0.050	36.22
LK GW LWD	6	-44.64	104.182	2.066	0.049	35.59
LK LWD	5	-46.18	104.351	2.236	0.045	32.70
LK H_P	5	-46.26	104.525	2.409	0.041	29.98
LK GW DT	6	-44.81	104.526	2.411	0.041	29.96
LK GW H_P	6	-44.85	104.592	2.477	0.040	28.99
LK GW DT LWD	7	-43.35	104.705	2.589	0.038	27.40
LK GW H_P LK*GW	7	-43.54	105.085	2.969	0.031	22.66
LK GW DT LK*GW	7	-43.67	105.337	3.221	0.027	19.97
LK DT LWD	6	-45.28	105.458	3.342	0.026	18.81
LK H_P LK*H_P	6	-45.75	106.395	4.280	0.016	11.77
LK GW H_P GW*H_P	7	-44.22	106.436	4.321	0.016	11.53
LK GW H_P LWD	7	-44.23	106.460	4.344	0.016	11.39
LK DT H_P	6	-45.91	106.708	4.593	0.014	10.06

Table C16. Estimates of fixed and random effects for the selected best fitting hierarchical linear models for biomass in lower FRB streams during spring.

Model:			90% Confidence Interval	
	Parameter estimate	Standard error	Lower	Upper
Link:				
Intercept	3.0605	0.2605	2.6073	3.5136
Link	<0.0001	0.0008	-0.0014	0.0014
Random effect	0.3440	0.2148	-0.0084	0.6963
Link, Groundwater, Drought, Groundwater*Drought:				
Intercept	2.4461	0.3889	1.7672	3.1250
Link	0.0003	0.0008	-0.0011	0.0017
Groundwater	1.1224	0.4182	0.3892	1.8556
Drought	0.3803	0.3071	-0.1581	0.9187
Groundwater*Drought	-1.0031	0.3974	-1.6998	-0.3064
Random effect	0.3886	0.1936	0.0711	0.7061
Link, Groundwater:				
Intercept	2.6648	0.3486	2.0562	3.2735
Link	0.0002	0.0008	-0.0011	0.0015
Groundwater	0.5637	0.3532	-0.0507	1.1781
Random effect	0.2812	0.1917	-0.0332	0.5956
Link, Groundwater, Link*Groundwater:				
Intercept	2.3390	0.3815	1.6702	3.0077
Link	0.0013	0.0010	-0.0004	0.0031
Groundwater	1.1255	0.4782	0.2937	1.9573
Link*Groundwater	-0.0023	0.0014	-0.0048	0.0002
Random effect	0.2059	0.1751	-0.0813	0.4930
Link, Drought:				
Intercept	3.1613	0.2885	2.6595	3.6631
Link	<0.0001	0.0008	-0.0014	0.0014
Drought	-0.1951	0.2318	-0.5997	0.2096
Random effect	0.3675	0.2181	0.0098	0.7252

Table C17. Predictor variables, number of parameters (K), log-likelihood, AIC_c, ΔAIC_c, Akaike weights (*w*), and percent of maximum Akaike weight for the confidence set of candidate models (*i*) predicting biomass in lower FRB streams during summer. See Table 4 for model parameter explanations.

Candidate Model	K	Log Likelihood	AIC_c	ΔAIC_c	w_i	Percent of Maximum w_i
LK GW LK*GW	6	-74.96	163.669	0.000	0.298	100.00
LK GW DT LK*GW	7	-73.74	163.872	0.203	0.269	90.35
LK GW H_P LK*GW	7	-73.92	164.215	0.546	0.226	76.10
LK DT LK*DT	6	-76.96	167.666	3.998	0.040	13.55

Table C18. Estimates of fixed and random effects for the selected best fitting hierarchical linear models for biomass in lower FRB streams during summer.

Model:			90% Confidence Interval	
	Parameter estimate	Standard error	Lower	Upper
Link, Groundwater, Link*Groundwater:				
Intercept	2.1560	0.3160	1.6020	2.7101
Link	0.0015	0.0008	0.0001	0.0029
Groundwater	1.2643	0.3961	0.5955	1.9331
Link*Groundwater	-0.0033	0.0012	-0.0053	-0.0014
Random effect	<0.0001			
Link, Groundwater, Drought, Link*Groundwater:				
Intercept	2.4405	0.3604	1.8087	3.0722
Link	0.0015	0.0008	0.0001	0.0029
Groundwater	1.2670	0.3879	0.6116	1.9223
Drought	-0.4267	0.2770	-0.8948	0.0414
Link*Groundwater	-0.0033	0.0011	-0.0052	-0.0013
Random effect	<0.0001			
Link, Groundwater, Habitat diversity, Link*Groundwater:				
Intercept	1.1420	0.7788	-0.2233	2.5073
Link	0.0015	0.0008	0.0001	0.0028
Groundwater	1.2811	0.3893	0.6234	1.9388
Habitat diversity	0.3967	0.2794	-0.0754	0.8688
Link*Groundwater	-0.0032	0.0012	-0.0052	-0.0013
Random effect	<0.0001			
Link, Drought, Link*Drought:				
Intercept	3.6683	0.3383	3.0797	4.2569
Link	-0.0021	0.0010	-0.0039	-0.0004
Drought	-1.0842	0.3726	-1.7143	-0.4541
Link*Drought	0.0027	0.0011	0.0008	0.0047
Random effect	0.1885	0.1625	-0.0781	0.4551