

FUNCTIONAL GROUPINGS OF STREAM FISHES:
SPATIOTEMPORAL VARIATION, PREDICTABILITY,
AND PATTERNS OF DIVERSITY

by

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ABSTRACT

Biodiversity and ecosystem function is a contemporary topic at the forefront of ecology. It is driven by the fundamental need to understand how the loss of biodiversity, which is occurring all around the world, affects goods and services obtained from ecosystems. The scientific literature indicates functional attributes of species strongly influence ecosystem properties; however, a lack of understanding exists regarding the relationship among functional diversity, taxonomic diversity, and community structure. As a result, this dissertation contributes to our understanding of the relationship between biodiversity and ecosystem function by analyzing the organization of stream-fish assemblages from a functional and taxonomic perspective and by synthesizing the relationship between the two aspects of biodiversity. I used a combination of previously published data, which covered broad biogeographic areas, and my own field work to address various issues on multiple spatial and temporal scales. I focused exclusively on stream-fish assemblages because they are one of the most underrepresented groups of animals in biodiversity and ecosystem function research and because they play an important role in aquatic ecosystems by removing other plants and animals from the community, actively produce fragments or feces containing the bodies of their prey, and by mechanically disturbing substrates, thereby increasing suspension of materials in the water column. In general, I found functional redundancy within stream-fish assemblages, with functional groups dividing niche space more evenly than species whether looking at the entire state, ecoregions, river basins, or individual locations, and the spatial and

temporal structure of stream-fish assemblages is similar for functional and taxonomic perspectives. These results indicate the need for future studies on biodiversity and ecosystem function to explicitly examine functional diversity, or at least incorporate functional attributes of individuals, in order to gain a holistic understanding.

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CHAPTER I

INTRODUCTION

Biodiversity, in its simplest terms, refers to the variety of life on earth. More specifically, it is “the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems” (Convention on Biological Diversity 1992). In other words, biodiversity is an all encompassing concept that includes aspects of genetic diversity, organismal diversity, and ecological diversity (Gaston and Spicer 1998). Genetic diversity is the combination of nucleotides, genes, and chromosomes found within and among populations. Organismal diversity is the composition and abundance of a particular level of taxonomic hierarchy occupying a given area at a given time. Ecological diversity is the variety of populations, communities, or ecosystems within a given area, including elements of niches and habitats. Each of these components is crucial to the holistic understanding of biodiversity.

Biodiversity is essential for human existence because we depend on other species and the ecosystems they create (Daily 1997). First, biodiversity provides us with particular ecosystem services, including energy transfer, nutrient cycling, and water cycling. For example, plants convert sunlight into organic energy and produce oxygen in the process, microorganisms decompose waste products and recycle nutrients, and insects, birds, and bats pollinate our crops. Second, biodiversity provides food, medicine,

and natural products for human consumption. Third, biodiversity has direct economic benefits. Studies have estimated that biodiversity provides an average of 33 trillion dollars a year to the global economy (Costanza et al. 1997). Fourth, biodiversity provides natural beauty, which has aesthetic, cultural, recreational, and spiritual values.

Despite the obvious benefits humans glean from increased biodiversity, we are major contributors to its alarming decline worldwide. Studies estimate that 50% of the species are heading for extinction within the next 50 years (Pimm and Raven 2000; Thomas et al. 2004). In general, this decrease is a direct result of human population growth and consumption (Lubchenco et al. 1991; Kearns 1997), habitat conversion and sprawl (McKinney 2002; Turner et al. 2004), exotic species invasions (McKinney and Lockwood 1999; Rahel 2002), exploitation (Bawa and Reinmar 1998; Coleman and Williams 2002), and environmental degradation (Koch and Mooney 1996; Vitousek et al. 1997). Regardless of the specific reason, the loss of biodiversity may have profound impacts on ecosystem level processes to the point where it negatively affects the quality of life. As a result, ecologists have focused much of their attention to understanding the relationship between biodiversity and ecosystem function.

Research on biodiversity and ecosystem function has exploded over the past 10 years and is now a dominant topic at the forefront of ecology. The first studies to document an effect of biodiversity on ecosystem function were published in the mid-1990s (Tilman and Downing 1994; Naeem et al. 1994). Naeem et al. (1994) conducted their study in an artificial ecosystem, called the Ecotron, comprised of primary producers, consumers, and predators. Each of the three trophic levels had low, medium, and high

biodiversity. A decrease in biodiversity resulted in a decrease in productivity and ecosystem buffering to perturbation. Tilman and Downing (1994) conducted their study in a grassland ecosystem at Cedar Creek Natural History Area, Minnesota. They used experimental treatments comprised of one to 24 species of plants and found that productivity as well as retention of soil nutrients increased with species richness. Although these studies did not go uncontested (e.g., Huston 1997), they laid the foundation for future research in biodiversity and ecosystem function.

Many studies since have demonstrated clearly a positive relationship between biodiversity and ecosystem function, whether they addressed resistance (Frank and McNaughton 1991; Tilman and Downing 1994; Tilman 1996), variability (McNaughton 1977; Tilman et al. 1996; Naeem and Li 1997), or function (Naeem et al. 1994; Tilman et al. 1996; McGrady-Steed et al. 1997; Wardle et al. 1997) of ecosystems. In fact, in a recent review of the effects of biodiversity on ecosystem function, Hooper et al. (2005) identified five generalities based on the scientific literature: (1) the functional characteristics of species strongly influence ecosystem properties, (2) a change in biota within an ecosystem alters ecosystem goods and services, (3) changes in species composition can differentially affect ecosystem properties depending on the type of ecosystem, (4) certain ecosystem properties are initially insensitive to decreases in biodiversity, and (5) more species are needed to maintain ecosystem function as spatial and temporal scales increase. Hooper et al. (2005) also discussed uncertainties that remain despite extensive research on biodiversity and ecosystem function, including the

need to further explore the relationship between functional diversity, taxonomic diversity, and community structure, and the need for additional studies in aquatic environments.

The overall objective of this dissertation is to examine the relationship between biodiversity and ecosystem function from a functional and taxonomic perspective. In Chapter 2, I examine the correlation between functional and taxonomic diversity of stream-fish assemblages from a macroecological perspective, determine whether broad-scale environmental variables can predict functional or taxonomic diversity, and determine whether functional or taxonomic diversity differ among ecoregions. In Chapter 3, I examine patterns of species abundance distributions from functional and taxonomic points of view to elucidate potential mechanisms by which species or functional groups partition niche space and to determine whether these mechanisms are scale dependent. In Chapter 4, I investigate spatial and temporal variation in the structure of stream-fish assemblages from functional and taxonomic perspectives. I also determine whether fine-scale environmental variables can predict functional or taxonomic diversity. These three chapters, in concert, provide a different perspective on the relationship between biodiversity and ecosystem function by incorporating aspects of both functional and taxonomic diversity.

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CHAPTER II
FUNCTIONAL AND TAXONOMIC DIVERSITY OF STREAM-FISH
ASSEMBLAGES ACROSS DIFFERENT ECOREGIONS

Abstract

The exact relationship between functional diversity, taxonomic diversity, and community structure remains elusive despite the extensive work conducted on biodiversity and ecosystem functioning. I analyzed a broad-scale data set on stream-fish assemblages to determine which aspects of taxonomic diversity correlate most strongly with functional diversity, whether certain broad-scale environmental variables can predict functional or taxonomic diversity, and whether functional or taxonomic diversity differ among ecoregions. Canonical correlation analysis between functional and taxonomic diversity demonstrated that the two aspects of biodiversity were correlated strongly, with over 50% of the variation in each suite of diversity measures being accounted for by the other suite. Partial least-squares (PLS) regression demonstrated that broad-scale biogeographic variables were poor predictors of functional and taxonomic diversity. Despite strong correlations between functional and taxonomic diversity, more ecoregions differed significantly based on taxonomic diversity than on functional diversity. Although the two aspects of biodiversity are somewhat correlated, they characterize different aspects of assemblage structure and provide complimentary insight into the overall relationship between biodiversity and ecosystem function.

Introduction

Biodiversity and ecosystem function is a contemporary topic at the forefront of ecology. It is driven by the fundamental need to understand how ecosystem processes are affected by the loss of biodiversity worldwide. Early in its infancy, much debate transpired in the ecological literature as to whether evidence supported the hypothesis of a positive relationship between biodiversity and ecosystem function (reviewed by Schwartz et al. 2000); however, many more studies since have found such a relationship for a variety of functional characteristics of ecosystems, such as resistance (Frank and McNaughton 1991; Tilman and Downing 1994; Tilman 1996), variability (McNaughton 1977; Tilman et al. 1996; Naeem and Li 1997), or function (Naeem et al. 1994; Tilman et al. 1996; McGrady-Steed et al. 1997; Wardle et al. 1997). Consequently, the emphasis of research on biodiversity and ecosystem function has shifted from simply determining whether biodiversity is important to ecosystem function to more of a holistic understanding (Rosenfeld 2002).

One promising avenue to gain a better understanding of how ecosystem function is affected by biodiversity is through macroecological analyses (Naeem and Wright 2003). Macroecology is a broad-scale, statistical approach to ecology that seeks to discover, describe, and explain patterns of species abundance, distribution, and diversity while making connections among different spatial and temporal scales (Brown 1995). Although macroecology traditionally has focused on taxonomic diversity, it extends easily to other aspects of biodiversity, including functional diversity. Functional diversity refers to the range of functions performed by organisms within an ecosystem

(Tilman 2001) and can be measured by quantifying the richness and abundance of groups of species with similar functional traits (Spehn et al. 2000). A functional trait is defined as “a specific character or phenotypic trait of a species that is associated with a biogeochemical process or ecosystem property under investigation” (Naeem and Wright 2003). Functional traits usually involve key aspects of an organism, such as its life history (Hooper and Vitousek 1997) or trophic status (Naeem and Li 1997); however, the most important traits governing an ecosystem likely will vary depending on temperature, soil or water conditions, precipitation, nutrient availability, or time since disturbance (Naeem and Wright 2003). Regardless of the functional trait considered, the exact relationships among functional diversity, taxonomic diversity, and community structure remains unresolved (Hooper et al. 2005).

The underlying goal of this study was to examine the relationship between functional and taxonomic diversity from a macroecological perspective and to interpret the findings in the context of current knowledge regarding the corresponding community structure. More specifically, the objectives of this study were to determine: (1) which aspects of taxonomic diversity correlate with functional diversity, (2) whether certain broad-scale environmental variables can predict functional or taxonomic diversity, and (3) whether functional or taxonomic diversity vary among ecoregions. This study uses stream-fish assemblages as a focal system because they are one of the most underrepresented groups of animals in biodiversity and ecosystem function research and because they play an important role in aquatic ecosystems by removing other plants or animals from the community, actively producing fragments or feces containing the bodies

of their prey, and by mechanically disturbing substrates, thereby increasing suspension of materials in the water column (Matthews 1998).

Materials and Methods

Data

I obtained data from fisheries surveys conducted by the Texas Parks and Wildlife Department (Linam et al. 2002). The surveys focused on the least disturbed streams of 11 different ecoregions of Texas, including all but one ecoregion described by Omernik (1987), and included 62 localities from 18 drainages. Biologists from Texas Parks and Wildlife sampled fish assemblages using seines (100% of sites), backpack electrofishing (81% of sites), and boat electrofishing (8% of sites) with gear choice depending on environmental characteristics such as flow regimes, water chemistry, and habitat availability. They sampled each locality until species accumulation peaked and sampled all habitats within a locality in relative proportion to their abundance. They sampled streams during the summer months (June through September) from 1988 through 1990. Data included a description of the sampling site, latitude and longitude, size of drainage basin (km^2), stream discharge (ft^3/s), and abundances of fish species at each site. From these data I constructed an environmental data set that included latitude, longitude, elevations, discharge, and basin area and a data set on taxonomic diversity.

Ecoregions of Texas

Twelve ecoregions are located within the state of Texas; however, biologists from the Texas Parks and Wildlife incorporated only 11 of them into their study because the Arizona/New Mexico Mountains barely extend into Texas and few perennial streams occur within the ecoregion. The remaining ecoregions are the Chihuahuan Desert, Western High Plains, Southwestern Tablelands, Central Great Plains, Central Oklahoma/Texas Plains, Edwards Plateau, Southern Texas Plains, Texas Blackland Prairies, East Central Texas Plains, Western Gulf Coastal Plain, and South Central Plains. The Chihuahuan Deserts ecoregion comprises broad basins and valleys where the vegetative cover is predominantly arid grass and shrub land. The Western High Plains comprises smooth plains with a high percentage of cropland and grama-buffalo grass. The Southwestern Tablelands is located in sub-humid grassland and semiarid range land with most natural vegetation comprising buffalo grass and sand shinnery oak. The Central Great Plains generally receives more precipitation than the Western High Plains and now primarily comprises cropland, although it once was covered with low trees and shrubs. The Central Oklahoma/Texas Plains ecoregion consists of little bluestem grassland with scattered oak trees with most of the area converted to rangeland and pastureland. The Edwards Plateau ecoregion contains a sparse network of relatively pristine perennial streams surrounded by juniper-oak savanna and mesquite-oak savanna. The Southern Texas Plains consists primarily of thorny brush, but contains a greater and more distinct fauna than elsewhere in Texas. The Texas Blackland Prairies has a fine textured clay soil that now contains a high percentage of cropland. The East Central

Texas Plains originally was covered by a post oak savanna but now is used as rangeland. The Western Gulf Coastal Plains are relatively flat grasslands with a high percentage of cropland. The South Central Plains is primarily forests and woodlands that are dominated by loblolly and shortleaf pine.

I obtained all descriptions of the ecoregions from Omernik (1987). However, the Texas Parks and Wildlife followed Omernik and Gallant (1989) and aggregated some of the ecoregions; this included consolidating the Central Great Plains, Texas Blackland Prairies, and Central Oklahoma/Texas Plains into the Subhumid Agriculture Plains as well as consolidating the East Central Texas Plains and South Central Plains into the South Central and Southern Humid, Mixed Land Use Region (Figure 2.1).

Formation of Functional Groups

To classify fish species into functional groups, I used a classification scheme proposed by William Matthews (1998) that emphasizes the organism's role in ecosystem processes. This classification scheme expanded traditional trophic groups (e.g., herbivore, piscivore, invertivore) to include the manner in which fishes affect aquatic ecosystems. Although this classification scheme has not been inspected for its general usefulness nor have the groups been tested for differences in ecosystem level processes (e.g., nutrient cycling), it provides an initial framework to examine patterns of functional diversity in stream fishes by examining what fish eat, where they find food, and how they consume resources (Matthews 1998). This classification scheme imposes an important distinction between fishes that physically disturb substrates from fishes that do not

disturb substrates, which should differentially affect ecosystem processes such as nutrient cycling. In addition to this dichotomy, Matthews incorporated information on the manner in which fishes feed. For example he distinguished suction piscivores from biting piscivores because suction piscivores generally swallow prey whole, whereas biting piscivores tend to leave fragments in the environment that other organisms can consume. Hence, this classification scheme is specifically designed to directly address issues regarding ecosystem function, whether it is aspects of decomposition, primary production, nutrient cycling, or energy flow.

The specific functional groups I used in this study were (1) grazers, (2) browsers, (3) benthic detritivores, (4) mud or sand sifter, (5) disturbance pickers, (6) scavengers, (7) egg eaters, (8) filter feeders, (9) surface feeders, (10) water-column particulate feeders, (11) benthic pickers, (12) snail crushers, (13) suction piscivores, and (14) biting piscivores. Grazers scrape materials (e.g., algae) from hard substrates such as rocks and woody debris. Browsers feed on plant materials that are suspended in the water column, directly affecting primary productivity. Benthic detritivores consume dead or decaying matter from the bottom of aquatic environments, thereby directly altering nutrient cycling. Mud or sand sifters consume soft sediments to sift out invertebrate food items, increasing the suspension of fine particulate organic matter. Disturbance pickers mechanically disturb substrates in order to feed on invertebrate prey while increasing the suspension of fine particulate organic matter. Scavengers feed on a variety of animal material, dead or alive, directly altering energy flow. Egg eaters consume eggs of other fishes, directly affecting the abundance of other functional groups. Filter feeders remove

micro-organisms from the water column, which directly impacts primary productivity and prey availability for other drift feeding fishes. Surface feeders consume invertebrates from the top of the water column, thereby indirectly affecting the abundance of phytoplankton that many invertebrates feed on in turn affecting primary productivity. Water column particulate feeders feed on invertebrates in the middle of the water column. Benthic pickers do not disturb the substrate like disturbance pickers, but they do consume invertebrate from the benthos. Snail crushers consume hard bodied invertebrates, such as snails and crayfish. Suction piscivores consume other fishes by swallowing prey whole, leaving no fragments for other organisms to consume. Biting piscivores, on the other hand, are messy eaters and leave fragments of fish in the environment.

I assigned fish species to as many functional groups as needed based on accounts in the literature that documented feeding habits, reproductive strategies, or habitat requirements (Appendix A). I classified many species into multiple functional groups to reflect their opportunistic feeding strategies and ontogenetic shifts in diet. For these fishes, I partitioned the total number of individuals equally into the multiple functional groups so as not to artificially inflate the ecological importance of generalist species. Species that belonged to only one functional group had all individuals placed into that group.

Quantification of Biodiversity

For each locality I estimated several ecological indices of assemblage structure, including richness (S), Shannon diversity (H), Camargo evenness (E), and Berger-Parker

dominance (D) because they characterize different aspects of community structure (Stevens and Willig 2002; Magurran 2004) I estimated richness by simply determining the number of species or functional groups collected at each locality. I calculated Shannon diversity as $H = -\sum p_i \ln p_i$, which simultaneously accounted for richness and evenness (Pielou 1975). I calculated Camargo evenness (Camargo 1995),

$$E = 1 - \left(\sum_{i=1}^S \sum_{j=i+1}^S \left[\frac{p_i - p_j}{S} \right] \right),$$

which measures the equability of species abundances or functional group abundances within a particular locality. Camargo evenness values range from 0, which characterizes an assemblage in which abundances differ greatly, to 1, which characterizes an assemblage in which all species or functional groups are equally abundant. Berger-Parker dominance (Berger and Parker 1970), $D = N_{\max} / N$, assesses the degree to which assemblage structure is dominated by the most abundant species or functional group. For comparative purposes, I inverted the Berger-Parker index values so that larger values represent lower dominance, or increased biodiversity (Magurran 2004). In each case, functional groups were weighted by proportional abundance rather than proportional richness.

Quantitative Analyses

I used canonical correlation analysis (CCA) to assess pairwise relationships between functional and taxonomic diversity. CCA allows for an investigation of the relationship between two sets of variables by calculating the linear combination from each set, called a canonical variable, such that the correlation between two canonical

variables is maximized (Rencher 1992). CCA continues to find orthogonal canonical correlations, which are independent of previous correlations, until the number of canonical correlations equals the number of variables in the smaller of the two data sets. Because the distributional properties of the estimates are known, statistical significance of the canonical variates was assessed using Wilks' λ (Tabachnick and Fidell 1996). CCA was conducted using SPSS v 9.0 software (SPSS Inc. 1998).

I used partial least squares (PLS) regression to formulate predictive models of functional diversity based on broad-scale environmental variables (i.e., elevation, latitude, longitude, size of drainage basin, and stream discharge). PLS is a less restrictive extension of the multiple linear regression model that is used when many factors (i.e., independent variables) and response variables (i.e., dependent variables) are involved, when factors or response variables are correlated, or when relationships between factors and response variables are not well-understood (Geladi and Kowalski 1986). However, disadvantages to PLS exist, including greater difficulty in interpreting results and an inability to assess statistical significance without utilizing a randomization procedure such as the bootstrap (Tobias 1997). Consequently, I used the predicted residual sum of squares with cross-validation as the test statistic. The number of latent variables (linear relationships between factors and response variables) extracted was chosen that corresponded with the minimum prediction error on the validation set. PLS was conducted using SAS v 9.1 software (SAS Institute Inc. 2004).

I used multivariate analysis of variance (MANOVA) to determine whether mean levels of functional and taxonomic diversity varied significantly among ecoregions. If a

significant difference was found, I conducted separate MANOVAs for all pairwise combinations of ecoregions to determine which ecoregions differed from other regions. To keep the experimental wise error rate constant at $\alpha = 0.05$, I adjusted the alpha level for each pairwise comparison using sequential Bonferroni adjustments (Rice 1989). MANOVAs were conducted using MATLAB v 6.0 software (Mathworks 1997).

Results

Functional and Taxonomic Diversity

Biodiversity of stream-fish assemblages from a functional point of view was fairly moderate (Table 2.1). Functional richness for the 62 localities ranged from 6 to 13 (mean \pm SD = 10.2 ± 1.4). Functional diversity ranged from 0.61 to 2.11 (1.632 ± 0.310). Functional evenness ranged from 0.17 to 0.68 (0.423 ± 0.106). Functional dominance ranged from 1.14 to 5.17 (0.339 ± 0.124). Functional richness was significantly and positively correlated with guild diversity ($r = 0.36, P = 0.004$). Functional diversity was positively correlated with functional evenness ($r = 0.79, P < 0.001$) and functional dominance ($r = 0.80, P < 0.001$). Functional evenness was positively correlated with functional dominance ($r = 0.79, P < 0.001$). All remaining correlations were non-significant.

Biodiversity of the stream-fish assemblages from a taxonomic point of view was also fairly moderate (Table 2.2). Taxonomic richness for the 62 localities ranged from 6 to 25 (13.7 ± 5.2). Taxonomic diversity ranged from 0.43 to 2.78 (1.514 ± 0.544). Taxonomic evenness ranged from 0.14 to 0.52 (0.308 ± 0.099). Taxonomic dominance

ranged from 1.09 to 5.64 (2.282 ± 1.009). Taxonomic richness was significantly and positively correlated with taxonomic diversity ($r = 0.73, P < 0.001$) and taxonomic dominance ($r = 0.50, P < 0.001$). Taxonomic diversity was positively correlated with taxonomic evenness ($r = 0.70, P < 0.001$) and taxonomic dominance ($r = 0.86, P < 0.001$). Taxonomic evenness was positively correlated with taxonomic dominance ($r = 0.79, P < 0.001$).

Canonical Correlation Analysis

Three significant canonical correlations were found to exist between functional and taxonomic diversity ($r = 0.864, P < 0.001$; $r = 0.663, P < 0.001$; $r = 0.410, P = 0.029$). The three canonical variates together accounted for 95% of the variation in functional diversity (i.e., richness, diversity, evenness, and dominance) and for 53% of the variation in taxonomic diversity. In general, each component of functional diversity correlated strongly to the corresponding component of taxonomic diversity (Table 2.3). Diversity contributed most highly to the first canonical variate, richness to the second canonical variate, and dominance to the third canonical variate.

Partial Least Squares Regression

Overall, PLS regression failed to account for a majority of the covariation in functional (Table 2.4) and taxonomic (Table 2.5) diversity. Two extracted factors accounted for a significant amount of the variation (10.68%) in functional diversity (Table 2.6). Longitude and elevation, which were inversely related, were the major

environmental variables that contributed to the first extracted factor; basin area, discharge, and latitude were minor contributors. Latitude was the environmental variable that loaded most highly on the second extracted factor, followed by longitude, discharge, basin area, and elevation. Two extracted factors accounted for a significant amount of the variation (22.45%) in taxonomic diversity (Table 2.6). Longitude and elevation were the main environment variables involved in producing the first extracted factor; basin area, discharge, and latitude were minor contributors. Latitude was important in structuring the second extracted factor, followed by longitude, discharge, basin area, and elevation.

Multivariate Analysis of Variance

Assemblage structure differed significantly among ecoregions with respect to functional ($F = 3.15$, $df = [24, 182]$, $P < 0.001$) and taxonomic ($F = 5.66$, $df = [24, 182]$, $P < 0.001$) diversity. Ad hoc MANOVAs with sequential Bonferroni adjustments of α for 21 pairwise comparisons revealed a significant difference in functional diversity between Mixed Land Use Region and Central Texas Plains ($P = 0.002$ at $\alpha = 0.002$). All remaining comparisons were non-significant. Pairwise differences in taxonomic diversity among ecoregions were more prevalent. Taxonomic diversity between Mixed Land Use Region and Subhumid Agriculture Plains ($P < 0.001$ at $\alpha = 0.002$), Mixed Land Use Region and Western High Plains ($P < 0.001$ at $\alpha = 0.003$), Mixed Land Use Region and Central Texas Plains ($P < 0.001$ at $\alpha = 0.003$), Mixed Land Use Region and Chihuahuan Deserts ($P = 0.001$ at $\alpha = 0.003$), Western Gulf Coast Plains and Mixed Land Use Region

($P = 0.001$ at $\alpha = 0.003$), and Western Gulf Coast Plains and Western High Plains ($P = 0.002$ at $\alpha = 0.003$). All remaining comparisons were non-significant. With the exception of one pairwise difference between Western Gulf Coast Plains and Western High Plains, all significant differences involved the Mixed Land Use Region ecoregion.

Discussion

Predicting Functional and Taxonomic Diversity

In a recent attempt to transform biodiversity and ecosystem function research from an inferential to a predictive science, Naeem and Wright (2003) advocated using “biogeographic methods,” or abiotic covariates of biodiversity, to predict the abundance and distribution of functional groups. The results of this study suggest that biogeographic variables (e.g., latitude, longitude, elevation, discharge, and basin area) might not be useful for predicting functional diversity of stream-fish assemblages. This is in contrast to a study conducted by Poff and Allan (1995), who examined the functional organization of fish assemblages in relation to hydrological variability. They analyzed 34 sites in Wisconsin and Minnesota, using clustering methods to identify two functionally similar groups of assemblages, and using discriminant analysis of hydrological data to predict the two functionally similar groups of assemblages. They based their functional attributes on trophic guild, stream size preference, current velocity preference, substratum preference, tolerance, and body morphology. They found that the hydrological data could separate the two groups of assemblages, which were associated with hydrologically variable sites or hydrologically stable sites. Another study suggesting that functional attributes of

assemblages can be predicted from hydrological data was that of Goldstein and Meador (2004). They classified 429 freshwater fish from the Mississippi River basin into 29 species-trait categories based on substrate preference, geomorphic preference, trophic ecology, locomotion morphology, reproductive strategy, and stream-size preference. They analyzed the relationships between these categories and stream size categories (i.e., small streams, small rivers, medium rivers, large rivers, variable). Their results suggest that fish community function is structured by differences in habitat and is different for large rivers versus small rivers and streams.

In this study the environmental variables were also not useful for predicting taxonomic diversity, although nearly twice as much of the variation in taxonomic diversity was accounted for than in functional diversity. These results contradict much of what is known about stream-fish assemblages. One of the most important advances in stream ecology was the formulation of the River Continuum Concept (Cummins 1974; Vannote et al. 1980), which hypothesizes that the physical structure of a stream channel in concert with flow regimes and energy input produces a consistent pattern of structure and function along a stream. This conceptual model provides testable predictions that have been supported repeatedly for stream fish communities (Matthews 1986; Pires et al. 1999; Hoeninghaus et al. 2003; Santoul et al. 2005). For example, Schlosser (1982) tested the predictions of the River Continuum Concept and found qualitative support for it. He observed consistent patterns in community structure through time that were associated with spatial changes along a stream. Habitat diversity and volume increased from riffle to pool environments and from upstream to downstream environments. Upstream and

riffle environments had low species richness and consisted primarily of young, small fishes. Generalized insectivores were the dominant trophic guild. Temporal stability of species richness, trophic structure, and age structure was low. Downstream and pool environments, on the other hand, had high species richness and consisted primarily of old, large fishes. The dominant trophic guilds were insectivore-piscivores and benthic insectivores. Temporal stability was high in regards to species richness, trophic structure, and age structure.

The discrepancy between the results of this study and those of other studies may involve an issue of scale. The environmental variables used in this study may have been too course-grained to adequately account for fine-scale data (Allen and Starr 1982; Rahel 1990), such as the locality-specific abundances of functional groups and species. For example, Poff and Allan (1995) collapsed all of their abundance data into binary form because they felt that the abundance data were too sensitive to sampling gear and effort. However, in my study only 15% of the variation in functional richness, which is based fundamentally on binary data, was accounted for by coarse-grained environmental variables. Taxonomic richness, on the other hand, had 40% of its variation accounted for by latitude, longitude, basin area, elevation, and discharge. The disparities between the two aspects of biodiversity may reside in the method of formation of functional groups. Eighty-one percent of the species in this study were classified into more than one functional group. Thirty-four percent of the species were assigned to 2 functional groups, 35% to 3 functional groups, 11% to 4 functional groups, and only 1% to 5 functional groups. Although stream fishes tend to be very plastic in their behavior and can exhibit

multiple traits that affect various ecosystem attributes, the fact that any species was a capable of being categorized into multiple functional groups may have masked the relationships between broad-scale environmental variables and functional diversity.

Correlation between Functional and Taxonomic Diversity

Many studies use taxonomic diversity as a surrogate for functional diversity. From a bottom-up approach, the concepts of niche differentiation and limiting similarity suggest that the functional traits of species must differ at some point. This implies that functional richness should increase as taxonomic richness increases, especially if functional richness broadens the range of functional traits present within an ecosystem (Schmid et al. 2002). Although this relationship would result in a positive correlation between functional and taxonomic diversity, taxonomic diversity should not be an adequate surrogate for functional diversity unless there is a linear increase in niche space coverage with increased species richness (Diaz and Cabido 2001). Diaz and Cabido (2001) discussed only two possible ways in which this could happen: the first involving the random occupation of niche space, and the second requiring the niche space to be uniformly occupied. The stream-fish assemblages used in this study are neither randomly nor uniformly distributed in niche space (Chapter 3). Consequently, taxonomic diversity should not be used as a surrogate for functional diversity of stream-fish assemblages, despite the high degree of correlation between the two aspects of biodiversity.

The high degree of correlation between functional diversity and taxonomic diversity may indicate a need for refining the formation of functional groups so that more

insight is gained into biodiversity and ecosystem function. Of course, the relationship between functional and taxonomic diversity is likely to be sensitive to the functional traits considered, the ecosystem function investigated, the degree of redundancy and singularity among species, the manner in which biotic interactions modify the dynamics of ecosystem function, and how biogeographical factors influence species composition, abundance, and distribution (Naeem and Wright 2003). These factors may hinder the ability to interpret the relationship between functional and taxonomic diversity from a macroecological perspective. I did observe functional redundancy in term of richness and diversity, but not in evenness or dominance (Figure 2.2). This redundancy would still produce a correlation between functional and taxonomic diversity, but the relationship would not be linear. Perhaps a non-linear analysis would demonstrate a different relationship between functional and taxonomic diversity; however, the objective of this study was to examine only the linear relationships among various aspects of biodiversity.

Differences in Functional and Taxonomic Diversity among Ecoregions

In general, ecoregions were much more different from one another in terms of taxonomic diversity than in functional diversity. The only ecoregion difference accounted for by functional diversity was between the Mixed Land Use region and Central Texas Plains. Although the Mixed Land Use region had a high functional richness, the abundances within functional groups were more even in the Central Texas Plains. The high evenness in the Central Texas Plains also resulted in a higher functional

diversity. This probably is due to the Mixed Land Use region being comprised primarily of piney woods whereas the Central Texas Plains is primarily grassland with only a small subset comprising of small shrubs and trees. The difference in vegetation would likely cause a dramatic difference in the amount of autochthonous and allochthonous energy within the streams, with the Central Texas Plains having more energy derived from autochthonous sources.

The Mixed Land Use region was significantly different from other ecoregions in terms of taxonomic diversity, with the exception of Southern Texas Plains; although the latter difference would have been significant without the sequential Bonferroni adjustment. The Mixed Land Use region had an average taxonomic richness of 21 species, which much greater than the other ecoregions. In fact, the next closest ecoregion was the Southern Texas Plain, with an average of 14 species. The Mixed Land Use region has much more precipitation that is more evenly spaced throughout the year than any of the other ecoregions, which results in a more constant environment. Stream segments having more constant environments generally have much higher species richness than those in highly variable environments (Horwitz 1978; Hutchison 1993).

Conclusions

Studies of biodiversity have taken center stage in ecology over the past 20 years. However, much of the current work on biodiversity focuses on taxonomic diversity rather than functional diversity. Although the two aspects of biodiversity are somewhat related, they actually characterize different aspects of assemblage structure and provide

complementary insight into the overall relationship between biodiversity and ecosystem function. In fact, the “functioning of an ecosystem is not governed by the phylogenetic content of its biota, but by the functional traits of individuals, the distribution and abundance of these individuals, and their biological activity” (Naeem and Wright 2003). Consequently, it is imperative that future studies addressing issues regarding biodiversity and ecosystem function make explicit use of functional groups, or at least incorporate the functional attributes of individuals. Although this study did not find a predictive relationship between broad-scale environmental variables and functional diversity, it does provide an initial examination of the relationship between functional and taxonomic diversity and their association with known concepts in stream-fish ecology. However, more work on aquatic systems is needed if a truly holistic understanding of biodiversity and ecosystem functioning is to emerge.

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Table 2.1. Functional diversity for each of the 62 localities sampled by the Texas Parks and Wildlife Department. Richness, diversity, evenness, and dominance correspond to number of functional groups, Shannon's diversity, Camargo's evenness, and Berger-Parker dominance indices, respectively (see text for more details).

Assemblage	Functional Diversity			
	Richness	Diversity	Evenness	Dominance
West Bernard Creek	13	1.30	0.23	2.29
West Mustang Creek	11	1.65	0.38	3.58
Arenosa Creek	8	0.91	0.28	2.09
Big Creek	11	1.96	0.53	4.79
West Carancahua Creek	11	1.39	0.29	2.72
Placedo Creek	8	1.12	0.32	2.27
Lake Creek	11	1.63	0.37	3.29
Little Cypress Creek	11	1.79	0.43	3.88
Catfish Creek	11	1.90	0.47	3.97
Big Cypress Creek	12	1.83	0.41	3.62
East Fork of the San Jacinto River	11	1.81	0.45	4.05
Keechi Creek	10	1.87	0.51	3.66
Piney Creek	12	1.66	0.33	2.84
Irons Bayou	11	1.91	0.47	3.68
Frazier Creek	12	1.89	0.43	4.07
White Oak Creek	11	1.71	0.41	3.67
Beech Creek	12	1.89	0.43	4.16
Black Cypress Creek	11	1.73	0.40	3.27
Wheelock Creek	11	1.90	0.47	3.72
Ponds Creek	8	1.10	0.32	2.19
San Miguel Creek	11	1.41	0.29	2.47
Sycamore Creek	13	1.86	0.40	2.19
Metate Creek	10	1.29	0.29	2.40
Pinto Creek	9	1.68	0.46	2.71
Cowhouse Creek	9	1.86	0.56	3.16
Medina River	10	1.63	0.41	3.49
South Llano River	9	1.56	0.44	3.56
Onion Creek	10	1.95	0.56	3.52

Table 2.1. Continued

Rocky Creek	10	1.66	0.42	2.20
Barton Creek	9	2.01	0.67	3.97
Little Blanco River	10	1.81	0.47	3.38
Oatmeal Creek	10	1.59	0.40	1.92
Little Barton Creek	9	1.95	0.68	5.17
Elm Creek	13	1.79	0.37	3.79
Spring Creek	10	1.77	0.46	3.35
Cummins Creek	11	1.64	0.36	3.02
Mill Creek	12	1.74	0.37	3.65
Clear Creek	12	1.92	0.43	3.16
Cottonwood Creek	11	1.48	0.33	3.15
Neils Creek	9	1.73	0.50	3.59
Deer Creek	12	1.85	0.41	3.11
West Rocky Creek	9	1.94	0.63	4.75
Steele Creek	9	1.75	0.50	3.70
Colony Creek	11	1.90	0.48	3.30
Deadman Creek	10	1.66	0.41	2.98
Auds Creek	9	1.42	0.38	2.42
Bluff Creek	10	1.73	0.46	4.11
Wilson Creek	10	2.11	0.66	4.65
Ioni Creek	8	1.81	0.62	3.86
Bluff Creek	8	1.54	0.46	2.89
Willis Creek	10	1.42	0.34	2.47
Geronimo Creek	10	1.75	0.45	2.84
Wolf Creek	9	1.81	0.54	4.07
McClellan Creek	8	1.55	0.52	3.95
Whitefish Creek	6	0.81	0.32	1.76
Lelia Lake Creek	9	1.51	0.45	3.74
Saddlers Creek	9	1.12	0.26	1.71
Devils River	9	1.50	0.41	3.38
Independence Creek	10	0.99	0.23	1.33
Alamito Creek	9	1.37	0.35	2.58
Terlingua Creek	12	1.79	0.40	3.78
Live Oak Creek	11	0.61	0.17	1.14

Table 2.2. Taxonomic diversity for each of the 62 localities sampled by the Texas Parks and Wildlife Department. Richness, diversity, evenness, and dominance correspond to number of functional groups, Shannon's diversity, Camargo's evenness, and Berger-Parker dominance indices, respectively (see text for details).

Assemblage	Taxonomic Diversity			
	Richness	Diversity	Evenness	Dominance
West Bernard Creek	16	1.04	0.19	1.29
West Mustang Creek	12	1.14	0.21	1.83
Arenosa Creek	9	0.43	0.16	1.09
Big Creek	15	1.58	0.26	2.52
West Carancahua Creek	12	0.77	0.14	1.38
Placedo Creek	9	0.57	0.17	1.16
Lake Creek	23	1.92	0.23	2.50
Little Cypress Creek	25	2.09	0.30	2.16
Catfish Creek	23	2.57	0.44	4.65
Big Cypress Creek	25	2.19	0.29	3.39
East Fork of the San Jacinto River	22	2.27	0.34	3.60
Keechi Creek	17	2.29	0.44	4.25
Piney Creek	22	1.90	0.29	1.87
Irons Bayou	21	2.56	0.47	4.97
Frazier Creek	21	2.35	0.39	3.12
White Oak Creek	20	2.23	0.36	3.65
Beech Creek	24	2.78	0.52	5.64
Black Cypress Creek	22	2.10	0.30	2.49
Wheelock Creek	16	2.16	0.42	3.04
Ponds Creek	13	0.68	0.14	1.17
San Miguel Creek	13	1.11	0.20	1.40
Sycamore Creek	21	2.25	0.38	2.55
Metate Creek	8	0.84	0.24	1.28
Pinto Creek	14	1.65	0.32	1.79
Cowhouse Creek	11	1.74	0.41	2.23
Medina River	14	1.60	0.28	1.93
South Llano River	14	1.30	0.21	1.89
Onion Creek	11	1.69	0.38	2.58
Rocky Creek	13	1.45	0.25	2.20

Table 2.2. Continued

Barton Creek	10	1.81	0.48	3.97
Little Blanco River	12	1.69	0.34	2.47
Oatmeal Creek	7	1.34	0.42	1.97
Little Barton Creek	11	1.45	0.29	2.11
Elm Creek	13	1.24	0.21	1.97
Spring Creek	12	1.30	0.25	1.55
Cummins Creek	21	1.36	0.16	1.72
Mill Creek	18	1.80	0.26	2.25
Clear Creek	16	1.73	0.30	1.89
Cottonwood Creek	11	0.95	0.19	1.65
Neils Creek	14	1.33	0.24	1.50
Deer Creek	14	1.55	0.27	1.80
West Rocky Creek	10	1.88	0.50	3.77
Steele Creek	13	1.35	0.27	1.51
Colony Creek	13	1.84	0.37	3.24
Deadman Creek	11	1.39	0.29	1.69
Auds Creek	11	0.96	0.22	1.29
Bluff Creek	9	1.72	0.48	3.36
Wilson Creek	13	1.93	0.41	3.09
Ioni Creek	10	1.64	0.41	2.03
Bluff Creek	7	1.21	0.38	1.61
Willis Creek	9	0.90	0.24	1.28
Geronimo Creek	10	1.65	0.40	2.51
Wolf Creek	8	1.59	0.48	2.97
McClellan Creek	8	1.14	0.33	2.07
Whitefish Creek	6	0.63	0.25	1.24
Lelia Lake Creek	6	0.92	0.36	1.96
Saddlers Creek	7	1.14	0.35	1.84
Devils River	12	0.97	0.19	1.30
Independence Creek	12	1.09	0.22	1.37
Alamito Creek	9	1.13	0.27	1.60
Terlingua Creek	10	1.40	0.31	2.15
Live Oak Creek	8	0.58	0.21	1.14

Table 2.3. Loadings from canonical correlation analysis between functional and taxonomic diversity.

	Canonical Variate			
	1	2	3	4
Functional richness	-0.479	0.763	-0.125	-0.416
Functional diversity	-0.979	-0.074	0.181	0.063
Functional evenness	-0.675	-0.604	0.416	0.078
Functional dominance	-0.672	-0.035	0.717	0.182
Taxonomic richness	-0.549	0.774	-0.032	-0.313
Taxonomic diversity	-0.916	0.170	0.153	-0.330
Taxonomic evenness	-0.653	-0.526	0.300	-0.455
Taxonomic dominance	-0.703	0.030	0.615	-0.355

Table 2.4. Partial least-squares (PLS) regression analysis of broad-scale functional diversity, with cross-validation.

Number of PLS factors	Percent variation accounted for				Cross-validation	
	Factors		Response		T2	P
	Current	Total	Current	Total		
0					9.24	0.046
1	43.49	43.49	5.27	5.27	18.85	<0.001
2	19.41	62.90	5.41	10.68	0.00	1.000
3	31.02	93.92	0.39	11.08	6.04	0.182
4	5.26	99.18	0.92	12.00	5.02	0.274
5	0.82	100.00	1.38	13.38	9.24	0.029

Table 2.5. Partial least-squares (PLS) regression analysis of broad-scale taxonomic diversity, with cross-validation.

Number of PLS factors	Percent variation accounted for				Cross-validation	
	Factors		Response		T2	P
	Current	Total	Current	Total		
0					9.16	0.036
1	42.27	42.27	16.44	16.44	9.57	0.036
2	29.33	71.60	6.01	22.45	3.81	0.468
3	22.58	94.18	2.66	25.11	4.30	0.386
4	3.13	97.31	3.05	28.16	0.00	1.000
5	2.69	100.00	2.24	30.40	8.86	0.035

Table 2.6. Loadings of environmental variables on extracted factors produced by partial least squares regression.

Factors	Functional Diversity		Guild Diversity	
	1	2	1	2
Latitude	-0.17	-0.95	-0.01	-0.84
Longitude	0.73	-0.32	0.81	-0.15
Elevation	-0.65	-0.11	-0.62	-0.32
Discharge	-0.14	-0.22	-0.06	0.29
Basin Area	-0.17	0.13	-0.16	0.41
<u>Response</u>				
Richness	0.77	0.36	0.77	0.20
Diversity	0.56	-0.40	0.51	-0.32
Evenness	0.02	-0.62	0.01	-0.81
Dominance	0.30	-0.57	0.38	-0.45



Figure 2.1. Ecoregions of Texas as used by Linam et al. (2002) in their study on the regionalization of indices of biotic integrity.

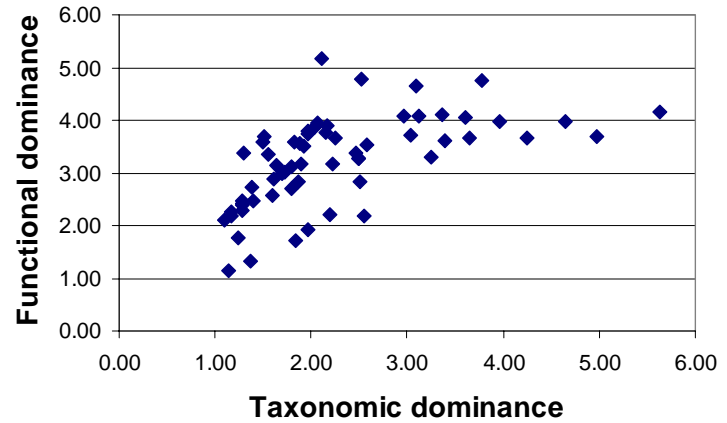
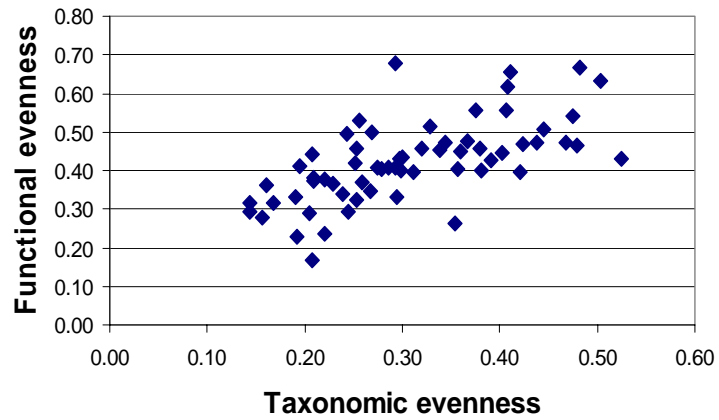
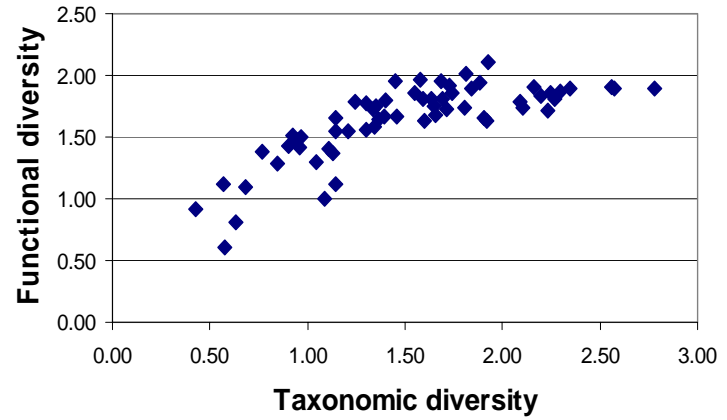
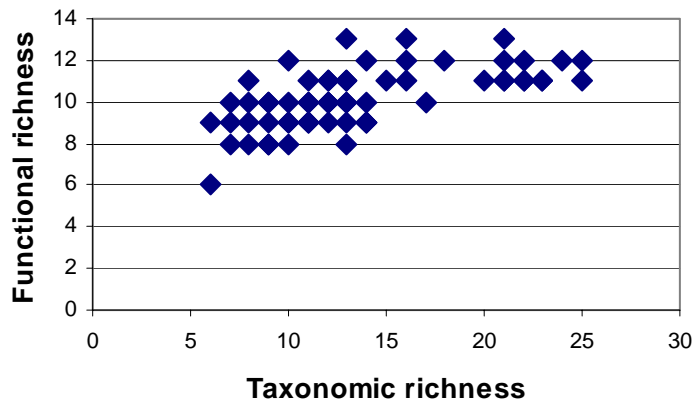


Figure 2.2. Scatterplots of various aspects of functional and taxonomic diversity.

CHAPTER III

MODELING STREAM-FISH ASSEMBLAGES WITH NICHE APPORTIONMENT

MODELS: PATTERNS, PROCESSES, AND SCALE DEPENDENCE

Abstract

Understanding patterns in terms of the mechanistic processes that produce them is the essence of ecology. However, many studies merely document non-random patterns of species coexistence without providing insight into the structuring mechanisms and their scale dependence. Moreover, very few studies address the mechanisms driving functional diversity. The objectives of this study were to document empirical patterns of species coexistence within stream-fish assemblages across a broad geographical region from functional and taxonomic perspectives, to elucidate the underlying processes that produce them, and to determine whether the structuring mechanisms are scale dependent. I gathered data from a report published by the Texas Parks and Wildlife that provides empirical species abundance distributions for 62 assemblages from seven ecoregions and 18 river basins. For each assemblage, I simulated observed species abundances using five previously published models that focus specifically on niche apportionment. These models included four stochastic variants of the Geometric Series (Dominance Preemption, Random Fraction, Broken-stick, and Dominance Decay) in which species abundances relate directly to niche breadth and one model (Random Assortment) in which abundances are independent of niche availability. To assess scale dependence, I pooled assemblages according to ecoregion, river basin, and the entire state. Patterns of niche apportionment for assemblages pooled according to river basin are more consistent

with local assemblages than pooled according to ecoregions or the entire state. Results suggest that niche apportionment may play a crucial role in structuring stream-fish assemblages and indicate functional groups divide niche space more evenly than species.

Introduction

The niche concept has been one of the most important contributions to community ecology, stimulating numerous theoretical and empirical studies. An ecological niche typically encompasses all the physical, chemical, and biological conditions required by a species for survival, growth, and reproduction. However, the exact definition of the niche has undergone several transformations. Grinnell (1917) originally defined it as the collection of sites where a species can live. Elton (1927) defined it as the function a species performs in the community to which it lives. These two definitions differ markedly in that one focused on where a species is found (Grinnell 1917) and the other focused on what the species actually does (Elton 1927). Hutchinson (1957) took a more sophisticated approach and defined a niche as a region (n -dimensional hypervolume) within the multi-dimensional space of environmental factors that are required by a species. This definition more closely resembles Grinnell's definition than Elton's and became popular because it suggested that ecologists could quantify and model an ecological niche. However, a contemporary understanding of an ecological niche should not ignore its functional aspects (Chase and Leibold 2003), especially considering the current emphasis in biodiversity and ecosystem function.

Understanding how species partition niche space can provide valuable insight into the mechanisms that structure local communities and how species coexist. One approach

to understanding niche partitioning involves the use of models. Models are extremely useful in ecology because they involve simplification and idealization, have internal structure, and generate empirical predictions (Pickett et al. 1994). A relatively new suite of models has been developed that specifically focuses on niche partitioning as an ecological mechanism (Tokeshi 1990; Tokeshi 1999). These models are stochastic variants of the geometric series and provide insight in how species subdivide niche space in order to coexist. Although these models have been used only within a taxonomic framework, there is no reason why they cannot be applied to functional groups as well, especially considering that the niche concept has a functional component associated with it (Elton 1927; Odum 1959).

Cummins (1974) first used the term ‘functional group’ in developing a classification scheme for feeding groups of macroinvertebrates that was partially independent of taxonomic identities. Cummins’ main goal was to develop a tool for addressing process-oriented questions in ecology, such as many contemporary questions directly pertaining to biodiversity and ecosystem function. The functional group concept is concerned with how different species process resources in order to provide a particular ecosystem function, which is different from the guild concept in which species utilize similar resources in similar ways in a competitive context (Blondel 2003). In stream-fish ecology, guilds are often used to simplify and classify multiple-species assemblages and have been used to examine local assemblage structure (Schlosser 1982; Bain et al. 1988; Douglas and Matthews 1992; Grossman et al. 1998), biotic integrity (Gorman and Karr 1978; Schleiger 2000; Smogor and Angermeier 2001), diet selection (Horwitz 1978; Schlosser 1985), habitat use (Leonard and Orth 1988; Aadland 1993; Zorn et al. 2002),

and reproductive strategies (Page and Swofford 1984). However, few studies have actually incorporated functional traits into studies of assemblage structure (but see Poff and Allan 1995; Goldstein and Meador 2004), and no published study has analyzed niche partitioning in stream fishes from a functional-group perspective.

The overall goal of this study was to understand how functional groups and species partition niche space. More specifically, the objectives were (1) to document empirical patterns of functional and taxonomic coexistence within stream-fish assemblages across a broad geographical region, (2) to elucidate the underlying processes that produce them, and (3) to determine whether the structuring mechanisms are scale dependent.

Materials and Methods

Data

I obtained data from fisheries surveys conducted by the Texas Parks and Wildlife (Linam et al. 2002). The surveys focused on the least disturbed streams of 11 different ecoregions of Texas, which included all but one ecoregion as described by Omernik (Omernik 1987), and included 62 localities from 18 drainages. Biologists from the Texas Parks and Wildlife sampled fish assemblages using seines (100% of sites), backpack electrofishing (81% of sites), and boat electrofishing (8% of sites) with gear choice depending on environmental characteristics such as flow regimes, water chemistry, and habitat availability. They sampled each locality until species accumulation peaked and sampled all habitats within a locality in relative proportion to their abundance. They sampled streams during the summer months (June through September) from 1988

through 1990. Data included a description of the sampling site, latitude and longitude, size of drainage basin (km²), stream discharge (ft³/s), and abundances of fish species at each site.

Ecoregions of Texas

Twelve ecoregions are located within the state of Texas; however, only 11 ecoregions were incorporated into the study by the Texas Parks and Wildlife because the Arizona/New Mexico Mountains barely extend into Texas and few perennial streams occur within the ecoregion. The remaining ecoregions include Chihuahuan Deserts, Western High Plains, Southwestern Tablelands, Central Great Plains, Central Oklahoma/Texas Plains, Edwards Plateau, Southern Texas Plains, Texas Blackland Prairies, East Central Texas Plains, Western Gulf Coastal Plain, and South Central Plains. The Chihuahuan Deserts ecoregion comprises broad basins and valleys where the vegetative cover is predominantly arid grass and shrubland. The Western High Plains comprises smooth plains with a high percentage of cropland and grama-buffalo grass. The Southwestern Tablelands is located in sub-humid grassland and semiarid range land with most natural vegetation comprising buffalo grass and shinnery. The Central Great Plains generally receives more precipitation than the Western High Plains and is comprised now primarily of cropland, although low trees and shrubs once covered it. The Central Oklahoma/Texas Plains ecoregion consists of little bluestem grassland with scattered oak trees with most of the area converted to rangeland and pastureland. The Edwards Plateau ecoregion contains a sparse network of perennial streams that are relatively pristine surrounded by juniper-oak savanna and mesquite-oak savanna. The

Southern Texas Plains primarily consists of thorny brush, but contains a greater and more distinct fauna than elsewhere in Texas. The Texas Blackland Prairies has a fine textured clay soil that now contains a high percent of cropland. The East Central Texas Plains originally was covered by a post oak savanna, but is now used as rangeland. The Western Gulf Coastal Plains are relatively flat grasslands with a high percentage of cropland. The South Central Plains is primarily forests and woodlands that are dominated by loblolly and shortleaf pine. All descriptions of the ecoregions were obtained from Omernik (Omernik 1987). However, the Texas Parks and Wildlife followed Omernik and Gallant (1989) and aggregated some of the ecoregions; this included consolidating the Central Great Plains, Texas Blackland Prairies, and Central Oklahoma/Texas Plains into the Subhumid Agriculture Plains as well as consolidating the East Central Texas Plains and South Central Plains into the South Central and Southern Humid, Mixed Land Use Region.

River Basins of Texas

Twenty-three river basins exist within the state of Texas (Figure 3.1); however, because Linam et al. (2002) focused on streams with entire watersheds located within an ecoregion, they only sampled fish assemblages from 18 river basins: the Brazos River basin (15 sites), Colorado River basin (9 sites), Rio Grande River basin (7 sites), Trinity River basin (5 sites), Red River basin (4 sites), Cypress Creek River basin (3 sites), Sabine River basin (3 sites), Guadalupe River basin (2 sites), Lavaca-Guadalupe River basin (2 sites), Neches River basin (2 sites), Nueces River basin (2 sites), San Jacinto River basin (2 sites), Brazos-Colorado River basin (1 site), Canadian River basin (1

sites), Colorado-Lavaca River basin (1 site), Lavaca River basin (1 site), San Antonio River basin (1 site), and Sulphur River basin (1 site).

Formation of Functional Groups

To classify fish species into functional groups, I used a classification scheme proposed by William Matthews (1998) that emphasizes the organism's role in ecosystem processes. This classification scheme expanded traditional trophic groups (e.g., herbivore, piscivore, invertivore) to include the manner in which fishes affect aquatic ecosystems. Although this classification scheme has not been inspected for its general usefulness nor have the groups been tested for differences in ecosystem level processes (e.g., nutrient cycling), it provides an initial framework to examine patterns of functional diversity in stream fishes by examining what fish eat, where they find food, and how they consume resources (Matthews 1998). This classification scheme imposes an important distinction between fishes that physically disturb substrates from fishes that do not disturb substrates, which should differentially affect ecosystem processes such as nutrient cycling. In addition to this dichotomy, Matthews incorporated information on the manner in which fishes feed. For example he distinguished suction piscivores from biting piscivores because suction piscivores generally swallow prey whole, whereas biting piscivores tend to leave fragments in the environment that other organisms can consume. Hence, this classification scheme is specifically designed to directly address issues regarding ecosystem function, whether it is aspects of decomposition, primary production, nutrient cycling, or energy flow.

The specific functional groups I used in this study were (1) grazers, (2) browsers, (3) benthic detritivores, (4) mud or sand sifter, (5) disturbance pickers, (6) scavengers, (7) egg eaters, (8) filter feeders, (9) surface feeders, (10) water-column particulate feeders, (11) benthic pickers, (12) snail crushers, (13) suction piscivores, and (14) biting piscivores. Grazers scrape materials (e.g., algae) from hard substrates such as rocks and woody debris. Browsers feed on plant materials that are suspended in the water column, directly affecting primary productivity. Benthic detritivores consume dead or decaying matter from the bottom of aquatic environments, thereby physically disturbing the substrate. Mud or sand sifters consume soft sediments to sift out invertebrate food items, increasing the suspension of fine particulate organic matter. Disturbance pickers mechanically disturb substrates in order to feed on invertebrate prey while increasing the suspension of fine particulate organic matter. Scavengers feed on a variety of animal material, dead or alive, directly altering energy flow. Egg eaters consume eggs of other fishes, directly affecting the abundance of other functional groups. Filter feeders remove micro-organisms from the water column, which directly impacts primary productivity and prey availability for other drift feeding fishes. Surface feeders consume invertebrates from the top of the water column, thereby indirectly affecting the abundance of phytoplankton that many invertebrates feed on in turn affecting primary productivity. Water column particulate feeders feed on invertebrates in the middle of the water column. Benthic pickers do not disturb the substrate like disturbance pickers, but they do consume invertebrate from the benthos. Snail crushers consume hard bodied invertebrates, such as snails and crayfish. Suction piscivores consume other fishes by swallowing prey whole,

leaving no fragments for other organisms to consume. Biting piscivores, on the other hand, are messy eaters and leave fragments of fish in the environment.

I assigned fish species to as many functional groups as needed based on accounts in the literature that documented feeding habits, reproductive strategies, or habitat requirements (Appendix A). I classified many species into multiple functional groups to reflect their opportunistic feeding strategies and ontogenetic shifts in diet. For these fishes, I partitioned the total number of individuals equally into the multiple functional groups so as not to artificially inflate the ecological importance of generalist species. Species that belonged to only one functional group had all individuals placed into that group.

Species-Abundance Distributions

The species-abundance distributions (SADs) were based on variations of the geometric series (i.e., uniform, dominance decay, random assortment, dominance preemption) in which niche apportionment is the primary focus of the model (Tokeshi 1990; Tokeshi 1999). Each model assumes that the fraction of niche space sequestered by a species is proportional to its relative abundance and that the niche space is subdivided sequentially. The models differ in how the available niche space is subdivided, resulting in varying degrees of evenness (Figure 3.2). The dominance-decay model (DD) is a stochastic model in which each species sequesters less than half of available niche space, but the exact amount is uniformly random between 0 and 0.5. DD describes a situation in which a new species invades the niche space of the most abundance species, thereby decreasing the amount of dominance within a system. The

broken-stick model (BS) is a stochastic model that describes a situation in which niche space is divided in a probabilistic manner, although it is often viewed as representing an assemblage containing species of equal competitive ability that are fighting for niche space (Tokeshi 1993; Magurran 2004). The random-fraction model (RF) is very similar to BS except each additional species uniformly chooses which available niche to sequester; thus, RF creates a more dominated distribution than BS. The random-assortment model (RA) results in abundances that vary independently from one another and are unrelated to niche breadth. Because this model is unrelated to niche breadth, it explicitly serves as the null model with which to compare the remaining models. The dominance-preemption model (DP) is the converse of the DD model in that each additional species sequesters more than half of the available niche, but the exact amount is uniformly random between 0.5 and 1. That is, DP describes a situation in which each additional species sequesters less niche space than its predecessors and consequently has a lower abundance.

Simulations

In order to assess the degree of fit between the expected abundance distributions and observed data, I ran 1000 iterations of each model and averaged the results to produce a representative abundance distribution. I then calculated the sum-of-squared differences between observed and expected values as a measure of lack-of-fit between the models and the data. Typically in model selection, the model with the lowest sum-of-squared differences is judged to be the best fitting model. However, one does not know whether that model fits the data significantly better than the other models. Consequently,

I repeated the above procedure using bootstrapped data with another 1000 iterations to produce 95% confidence intervals around the original sum-of-squared differences. I then used an One-way, Model I Analysis of Variance procedure based on confidence intervals (Bird 2004; Strauss and Higgins, unpublished manuscript) to determine whether the models differed significantly in their fit to the empirical data. All simulations were conducted using MATLAB v 6.0 software (Mathworks 1997).

Results

Niche-partitioning models differed in their fit with empirical data, whether local assemblages were analyzed separately or whether assemblages were pooled by river basin, ecoregion, or for the entire state (Figure 3.3). Moreover, the best-fitting models were different for functional group abundances (Table 3.1) than for species abundances (Table 3.2). When I combined all of the assemblages from across the state, the BS model best fit the data from a functional perspective, while the RF model best fit the data from a taxonomic perspective. When pooled according to ecoregion, BS was the best-fitting model of functional group abundance for all ecoregions except the Western High Plains in which the RF and RA models fit the Western High Plains equally well. That is, one cannot distinguish between the two models for the Western High Plains. The RA model best described species abundances in the Western Gulf Coast Plains and the Western High Plains ecoregions. The RF model fit the species-abundance distributions best in the remaining ecoregions. When pooled according to river basin, the best-fitting models were more widely dispersed than pooled according to ecoregion from the functional and taxonomic perspective; however, the RF model fit a majority of the river basins in both

cases. The best-fitting models for the individual localities were quite different between the functional and taxonomic aspect. In general, functional groups were distributed more evenly in niche space and were characterized by models such as the dominance decay and broken-stick mechanisms; whereas species were more dominant in abundances and characterized by models closer to the dominance preemption end of the spectrum, including the random assortment model.

Discussion

Understanding patterns in terms of the mechanistic processes that produce them is the essence of ecology. However, many studies merely document non-random patterns of species coexistence without providing insight into the structuring mechanisms and their scale dependence. Although the results of this study suggest that stream fishes are plastic in how they partition available niche space from both functional and taxonomic perspectives, it does provide insight into potential structuring mechanisms. Functional groups divide niche space more evenly than individual species regardless of spatial scale. Hence, the underlying mechanisms that seem to structure stream-fish assemblages from a functional perspective are those that result in fairly even abundance distributions, such as the dominance decay and broken-stick models. Conversely, mechanisms resulting in dominant abundance distributions (e.g., dominance preemption) are more likely to structure the taxonomic aspect of stream-fish assemblages. Of course, the mechanism used and described in this study focus on community-wide processes, which is necessary for macroecological analyses, although other fine-scale mechanism may be responsible

for structuring local assemblages (e.g., behavioral mechanisms that incorporate aspects of habitat selection and predator avoidance).

Although this study focused specifically on niche based models, one cannot rule out the possibility that dispersal based-models (e.g., Hubbell 2001) are better suited for stream-fish assemblages, at least from the taxonomic perspective. Hubbell's dispersal-based model has received criticisms for assuming that species are identical in birth, death, migration, and speciation rates (Abrams 2001; Levine 2002). However, the resulting abundance distributions seem like they could provide a good fit for the data used in this study. In general, Hubbell's model results in a few highly abundant species, many species with intermediate abundance, and a few rare species, giving it a characteristic S-shaped pattern (Hubbell 2001). This pattern is consistent with observed species abundance distributions of stream fish in Texas. Hubbell's dispersal model could potentially fit the functional group abundances as well, but the niche concept is probably more applicable than the dispersal concept due to the functional component associated with the niche. However, Gaston and Chown (2005) explore reasons why neutral theory might be relevant to functional ecology.

Previous studies have suggested that niche space increases with habitat complexity in stream-fish assemblages (Willis et al. 2005). More than likely, this would decrease taxonomic evenness, thereby shifting the potential structuring mechanisms to more of a dominance-preemption model rather than a dominance-decay model. The anticipated effect on functional groups, however, is not as clear. Assuming that the system does not exhibit functional redundancy, the increase in species richness should result in an increase in functional richness, in which case the structuring mechanism

should shift towards the dominance-preemption end of the model spectrum. If the system is functionally redundant, the effect of adding species is case-specific, depending on the species added to the community. If the new species is functionally redundant with another species, then it would affect the abundance of that group rather than adding an entirely new group. However, if the species is not functionally redundant, then a new functional group is added to the assemblage. Either scenario could affect the abundance distribution, which could in turn alter the inferred structuring mechanisms.

Scale dependence has become a dominant topic in contemporary ecology (Weins 1989; Levin 1992). This increased interest in scale is driven by the need to integrate disparate subfields within ecology (Pickett et al. 1994). However, one must be cautious when pooling data and looking at broader scales than what organisms actually experience daily. First, studies should account for historical factors when pooling data. For example, pooling stream-fish assemblages according to ecoregions ignores the fact that species cannot realistically move from one river basin to another; whereas, pooling assemblages according to river basin allows for the fact that species can theoretically move between upstream and downstream reaches. Second, pooling assemblages from various localities increases the likelihood that different dominant species occur within the broader scale. This amalgamation of dominant species will more than likely increase the evenness of the overall abundance distribution. The broader the spatial and temporal scale, the bigger influence this will have on the overall abundance distribution.

Much of ecology is devoted to elucidating the underlying mechanisms that structure natural communities and to determining whether those mechanisms are scale dependent. The results of this study indicate that no one mechanism structures stream-

fish assemblages across broad geographic areas; instead, underlying mechanisms are specific to certain localities and are dependent on whether functional or taxonomic diversity is considered. This emphasizes the need to incorporate multiple aspects of biodiversity and the need for macroecological analyses. However, one must use extreme caution when interpreting results of broad-scale analyses because the structuring mechanisms may be scale dependent as in the case with stream-fish assemblages. Nevertheless, macroecological analyses of various aspects of biodiversity are necessary if a true understanding of structuring mechanisms is to emerge.

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Table 3.1. Relative difference between each of the niche partitioning models and functional group abundance distributions. Abbreviations for models are dominance decay (DD), broken-stick (BS), random fraction (RF), random assortment (RA), and dominance preemption (DP). Boldface numbers indicate the best fit model or models.

Scale	DD	BS	RF	RA	DP
<u>State</u>					
Texas	0.05 ^a	0.01^b	0.11 ^c	0.19 ^d	0.64 ^e
<u>Ecoregions</u>					
Western Gulf Coast Plains	0.16 ^a	0.07^b	0.10 ^c	0.12 ^d	0.55 ^e
Mixed Land Use Region	0.09 ^a	0.03^b	0.11 ^c	0.16 ^d	0.60 ^e
Southern Texas Plains	0.08 ^a	0.03^b	0.11 ^c	0.16 ^d	0.62 ^e
Central Texas Plains	0.03 ^a	0.02^b	0.14 ^c	0.20 ^d	0.62 ^e
Subhumid Agriculture Plains	0.07 ^a	0.02^b	0.10 ^c	0.18 ^d	0.63 ^e
Western High Plains	0.36 ^a	0.15 ^b	0.04^c	0.03^c	0.42 ^a
Southern Deserts	0.15 ^a	0.06^b	0.09 ^c	0.12 ^d	0.58 ^e
<u>River Basin</u>					
Brazos	0.04 ^a	0.01^b	0.13 ^c	0.20 ^d	0.63 ^e
Brazos-Colorado	0.36 ^a	0.21 ^b	0.08^c	0.06^c	0.29 ^a
Canadian	0.02^a	0.02^a	0.16 ^b	0.17 ^b	0.62 ^c
Colorado	0.04 ^a	0.01^b	0.13 ^c	0.20 ^d	0.62 ^e
Colorado-Lavaca	0.23 ^a	0.11 ^b	0.10 ^b	0.08^c	0.48 ^d
Cypress Creek	0.07 ^a	0.02^b	0.11 ^c	0.16 ^d	0.63 ^e
Guadalupe	0.11 ^a	0.02^b	0.08 ^a	0.14 ^a	0.65 ^c
Lavaca	0.11 ^a	0.05^b	0.12 ^a	0.14 ^a	0.58 ^c
Lavaca-Guadalupe	0.32 ^a	0.20 ^b	0.12 ^c	0.09^d	0.26 ^e
Neches	0.11 ^a	0.03^b	0.10 ^a	0.14 ^a	0.62 ^c
Nueces	0.33 ^a	0.18 ^b	0.09^c	0.07^c	0.34 ^a
Red	0.37 ^a	0.16 ^b	0.04^c	0.03^c	0.40 ^a
Rio Grande	0.16 ^a	0.05^b	0.07 ^c	0.12 ^d	0.60 ^e
Sabine	0.08 ^a	0.03^b	0.11 ^c	0.17 ^d	0.62 ^e
San Antonio	0.10 ^a	0.05^b	0.15 ^a	0.13 ^a	0.57 ^c
San Jacinto	0.13 ^a	0.05^b	0.10 ^a	0.13 ^a	0.60 ^c

Table 3.1. Continued

Sulphur	0.29 ^a	0.15 ^b	0.11 ^b	0.08^c	0.37 ^a
Trinity	0.03 ^a	0.01^b	0.13 ^c	0.19 ^d	0.64 ^e
<u>Locality</u>					
West Bernard Creek	0.36 ^a	0.21 ^b	0.08^c	0.06^c	0.28 ^a
West Mustang Creek	0.11 ^a	0.05^b	0.12 ^a	0.14 ^a	0.58 ^c
Arenosa Creek	0.32 ^a	0.20 ^b	0.13 ^c	0.10^d	0.26 ^e
Big Creek	0.02^a	0.02^a	0.15 ^b	0.20 ^c	0.62 ^d
West Carancahua Creek	0.24 ^a	0.11 ^b	0.10 ^b	0.08^c	0.47 ^d
Placedo Creek	0.29^a	0.16^a	0.12^a	0.09^a	0.33 ^b
Lake Creek	0.14 ^a	0.05^b	0.10 ^a	0.12 ^a	0.58 ^c
Little Cypress Creek	0.05^a	0.02^a	0.14 ^b	0.16 ^b	0.63 ^c
Catfish Creek	0.05^a	0.02^a	0.13 ^b	0.17 ^b	0.62 ^c
Big Cypress Creek	0.08 ^a	0.02^b	0.11 ^a	0.16 ^c	0.64 ^d
East Fork of the San Jacinto River	0.02^a	0.02^a	0.16 ^b	0.18 ^b	0.62 ^c
Keechi Creek	0.03^a	0.02^a	0.15 ^b	0.16 ^b	0.65 ^c
Piney Creek	0.18^a	0.05^a	0.08^a	0.08^a	0.61 ^b
Irons Bayou	0.04^a	0.01^a	0.12 ^b	0.16 ^b	0.66 ^c
Frazier Creek	0.06^a	0.02^a	0.13 ^b	0.16 ^b	0.62 ^c
White Oak Creek	0.07 ^a	0.03^b	0.13 ^a	0.15 ^a	0.61 ^c
Beech Creek	0.05^a	0.03^a	0.14 ^b	0.17 ^b	0.61 ^c
Black Cypress Creek	0.08 ^a	0.02^b	0.11 ^a	0.14 ^a	0.65 ^c
Wheelock Creek	0.06 ^a	0.02^b	0.12 ^a	0.16 ^c	0.64 ^d
Ponds Creek	0.32 ^a	0.18 ^b	0.13 ^c	0.09^d	0.28 ^a
San Miguel Creek	0.31 ^a	0.15 ^b	0.08^c	0.06^c	0.40 ^a
Sycamore Creek	0.38 ^a	0.18 ^b	0.02^c	0.07 ^d	0.35 ^a
Metate Creek	0.29^a	0.16^a	0.11^a	0.08^a	0.37^a
Pinto Creek	0.18^a	0.05^a	0.08^a	0.08^a	0.62 ^b
Cowhouse Creek	0.06 ^a	0.00^b	0.12 ^a	0.14 ^a	0.68 ^c
Medina River	0.11 ^a	0.05^b	0.13 ^a	0.14 ^a	0.57 ^c
South Llano River	0.08 ^a	0.05^b	0.15 ^c	0.14 ^c	0.57 ^d
Onion Creek	0.03^a	0.01^a	0.15 ^b	0.17 ^b	0.65 ^c
Rocky Creek	0.30 ^a	0.10^b	0.05^b	0.09 ^c	0.45 ^a
Barton Creek	0.01^a	0.02^a	0.16 ^b	0.19 ^b	0.62 ^c

Table 3.1. Continued

Little Blanco River	0.06 ^a	0.01^b	0.12 ^a	0.14 ^a	0.66 ^c
Oatmeal Creek	0.43 ^a	0.21 ^b	0.03^c	0.07^c	0.26 ^a
Little Barton Creek	0.01^a	0.04 ^b	0.19 ^c	0.21 ^d	0.55 ^e
Elm Creek	0.07 ^a	0.02^b	0.13 ^c	0.16 ^d	0.62 ^e
Spring Creek	0.08 ^a	0.02^b	0.12 ^a	0.14 ^a	0.64 ^c
Cummins Creek	0.18 ^a	0.06^b	0.09^b	0.10^b	0.57 ^c
Mill Creek	0.09 ^a	0.04^b	0.12 ^a	0.14 ^c	0.62 ^d
Clear Creek	0.14^a	0.04^a	0.08^a	0.12^a	0.61 ^b
Cottonwood Creek	0.15 ^a	0.07^b	0.11 ^c	0.12 ^c	0.55 ^d
Neils Creek	0.05 ^a	0.02^a	0.15 ^b	0.15 ^b	0.63 ^c
Deer Creek	0.15 ^a	0.04^b	0.09 ^a	0.11 ^a	0.60 ^c
West Rocky Creek	0.01^a	0.03^a	0.19 ^b	0.18 ^b	0.59 ^c
Steele Creek	0.06^a	0.03^a	0.14 ^b	0.15 ^b	0.62 ^c
Colony Creek	0.07 ^a	0.01^b	0.12 ^c	0.16 ^d	0.64 ^e
Deadman Creek	0.15^a	0.05^a	0.10^a	0.10^a	0.60 ^b
Auds Creek	0.28 ^a	0.14 ^b	0.11 ^b	0.08^c	0.38 ^a
Bluff Creek	0.04^a	0.03^a	0.17 ^b	0.17 ^b	0.59 ^c
Wilson Creek	0.01^a	0.02^a	0.17 ^b	0.20 ^b	0.61 ^c
Ioni Creek	0.01^a	0.02^a	0.17 ^b	0.16 ^b	0.64 ^c
Bluff Creek	0.14^a	0.06^a	0.13^a	0.10^a	0.57 ^b
Willis Creek	0.29^a	0.16^a	0.10^a	0.08^a	0.37 ^b
Geronimo Creek	0.14^a	0.03^a	0.10^a	0.12^a	0.62 ^b
Wolf Creek	0.03^a	0.02^a	0.16 ^b	0.17 ^b	0.62 ^c
McClellan Creek	0.05^a	0.05^a	0.18 ^b	0.16 ^b	0.56 ^c
Whitefish Creek	0.39 ^a	0.20 ^b	0.11^c	0.10^c	0.19 ^b
Lelia Lake Creek	0.08^a	0.06^a	0.16 ^b	0.15 ^b	0.55 ^c
Saddlers Creek	0.53 ^a	0.27 ^b	0.04^c	0.03^c	0.12^c
Devils River	0.11 ^a	0.07^b	0.15 ^c	0.13 ^a	0.53 ^d
Independence Creek	0.46 ^a	0.30 ^b	0.11 ^c	0.12 ^c	0.01^d
Alamito Creek	0.21 ^a	0.08^b	0.10^b	0.08^b	0.53 ^c
Terlingua Creek	0.08 ^a	0.03^b	0.12 ^a	0.16 ^c	0.62 ^d
Live Oak Creek	0.39 ^a	0.29 ^b	0.15 ^c	0.14 ^c	0.03^d

Table 3.2. Relative difference between each of the niche partitioning models and species abundance distributions. Abbreviations for models are dominance decay (DD), brokenstick (BS), random fraction (RF), random assortment (RA), and dominance preemption (DP). Boldface numbers indicate the best fit model or models.

Scale	DD	BS	RF	RA	DP
State					
Texas	0.22 ^a	0.16 ^b	0.01^c	0.12 ^d	0.48 ^e
Ecoregions					
Western Gulf Coast Plains	0.46 ^a	0.33 ^b	0.09 ^c	0.04^d	0.08 ^c
Mixed Land Use Region	0.18 ^a	0.11 ^b	0.01^c	0.16 ^d	0.54 ^e
Southern Texas Plains	0.23 ^a	0.12 ^b	0.01^c	0.12 ^b	0.52 ^d
Central Texas Plains	0.15 ^a	0.06 ^b	0.05^c	0.16 ^a	0.58 ^d
Subhumid Agriculture Plains	0.33 ^a	0.23 ^b	0.02^c	0.05 ^d	0.37 ^e
Western High Plains	0.54 ^a	0.32 ^b	0.04 ^c	0.02^d	0.08 ^e
Southern Deserts	0.18 ^a	0.09 ^b	0.04^c	0.13 ^d	0.55 ^e
River Basin					
Brazos	0.26 ^a	0.17 ^b	0.04^c	0.09 ^d	0.44 ^e
Brazos-Colorado	0.43 ^a	0.32 ^b	0.13 ^c	0.11 ^d	0.01^e
Canadian	0.10^a	0.03^a	0.13^a	0.10^a	0.64 ^b
Colorado	0.11 ^a	0.05^b	0.07^c	0.18 ^d	0.59 ^e
Colorado-Lavaca	0.49 ^a	0.32 ^b	0.11 ^c	0.08 ^d	0.00^e
Cypress Creek	0.23 ^a	0.13 ^b	0.02^c	0.11 ^b	0.51 ^d
Guadalupe	0.27 ^a	0.13 ^b	0.02^c	0.10 ^b	0.48 ^d
Lavaca	0.48 ^a	0.28 ^b	0.07 ^c	0.03^d	0.13 ^e
Lavaca-Guadalupe	0.39 ^a	0.30 ^b	0.14 ^c	0.14 ^c	0.03^d
Neches	0.23 ^a	0.13 ^a	0.03^b	0.15 ^a	0.46 ^c
Nueces	0.44 ^a	0.32 ^b	0.13 ^c	0.10 ^d	0.02^e
Red	0.54 ^a	0.32 ^b	0.05^c	0.03^c	0.06^c
Rio Grande	0.19 ^a	0.10 ^b	0.03^c	0.14 ^d	0.54 ^e
Sabine	0.09 ^a	0.04^b	0.05^b	0.20 ^c	0.63 ^d
San Antonio	0.49 ^a	0.27 ^b	0.02^c	0.03^c	0.19 ^b
San Jacinto	0.32 ^a	0.18 ^b	0.00^c	0.08 ^d	0.42 ^e

Table 3.2. Continued

Sulphur	0.43 ^a	0.30 ^b	0.13 ^c	0.12 ^c	0.02^d
Trinity	0.04 ^a	0.01^b	0.08 ^c	0.24 ^d	0.63 ^e
<u>Locality</u>					
West Bernard Creek	0.43 ^a	0.32 ^b	0.13 ^c	0.11 ^d	0.01^e
West Mustang Creek	0.48 ^a	0.28 ^b	0.06 ^c	0.03^d	0.14 ^e
Arenosa Creek	0.38 ^a	0.28 ^b	0.15 ^c	0.15 ^c	0.03^d
Big Creek	0.31 ^a	0.15 ^b	0.04^c	0.06^c	0.44 ^d
West Carancahua Creek	0.49 ^a	0.33 ^b	0.10 ^c	0.08 ^d	0.00^e
Placedo Creek	0.42 ^a	0.29 ^b	0.13 ^c	0.14 ^d	0.02^e
Lake Creek	0.36 ^a	0.20 ^b	0.00^c	0.04 ^d	0.39 ^a
Little Cypress Creek	0.42 ^a	0.27 ^b	0.03^c	0.05^c	0.24 ^b
Catfish Creek	0.07 ^a	0.02^b	0.09 ^a	0.20 ^c	0.63 ^d
Big Cypress Creek	0.22 ^a	0.11 ^b	0.03^c	0.11 ^b	0.53 ^d
East Fork	0.15 ^a	0.06 ^a	0.04^b	0.14 ^a	0.61 ^c
Keechi Creek	0.08^a	0.02^a	0.09 ^b	0.18 ^c	0.64 ^d
Piney Creek	0.45 ^a	0.31 ^b	0.06^c	0.06^c	0.12^c
Irons Bayou	0.04 ^a	0.00^b	0.10 ^a	0.22 ^c	0.64 ^d
Frazier Creek	0.17 ^a	0.07 ^a	0.04^b	0.15 ^a	0.57 ^c
White Oak Creek	0.15^a	0.05^a	0.05^a	0.14 ^b	0.61 ^c
Beech Creek	0.03^a	0.00^a	0.10 ^b	0.23 ^c	0.63 ^d
Black Cypress Creek	0.35 ^a	0.18 ^a	0.00^b	0.06 ^c	0.41 ^d
Wheelock Creek	0.18^a	0.06^a	0.05^a	0.12^a	0.59 ^b
Ponds Creek	0.40 ^a	0.31 ^b	0.14 ^c	0.13 ^d	0.02^e
San Miguel Creek	0.47 ^a	0.32 ^b	0.10 ^c	0.09 ^c	0.01^d
Sycamore Creek	0.29 ^a	0.15 ^b	0.03^c	0.11 ^b	0.42 ^a
Metate Creek	0.44 ^a	0.29 ^b	0.12 ^c	0.14 ^d	0.02^e
Pinto Creek	0.47 ^a	0.28 ^b	0.05^c	0.07^c	0.12^c
Cowhouse Creek	0.37 ^a	0.15 ^b	0.02^c	0.06 ^b	0.41 ^a
Medina River	0.49 ^a	0.28 ^b	0.02^c	0.03^c	0.18 ^b
South Llano River	0.50 ^a	0.29 ^b	0.05 ^c	0.02^d	0.15 ^e
Onion Creek	0.27 ^a	0.10^b	0.05^b	0.06^b	0.52 ^c
Rocky Creek	0.43 ^a	0.22 ^b	0.04^c	0.02^c	0.30 ^b
Barton Creek	0.07^a	0.04^a	0.14 ^b	0.16 ^b	0.60 ^c

Table 3.2. Continued

Little Blanco River	0.31 ^a	0.12^b	0.03^b	0.05^b	0.49 ^a
Oatmeal Creek	0.45 ^a	0.14 ^b	0.01^c	0.01^c	0.39 ^a
Little Barton Creek	0.45 ^a	0.20 ^b	0.01^c	0.01^c	0.33 ^a
Elm Creek	0.48 ^a	0.27 ^b	0.04 ^c	0.01^d	0.20 ^e
Spring Creek	0.49 ^a	0.31 ^b	0.08^c	0.08^c	0.04^c
Cummins Creek	0.50 ^a	0.35 ^b	0.07 ^c	0.02^d	0.05 ^c
Mill Creek	0.43 ^a	0.23 ^b	0.00^c	0.03 ^d	0.32 ^a
Clear Creek	0.48 ^a	0.28 ^b	0.04^c	0.05^c	0.15^c
Cottonwood Creek	0.50 ^a	0.30 ^b	0.08 ^c	0.05^d	0.06 ^c
Neils Creek	0.47 ^a	0.32 ^b	0.09 ^c	0.09 ^c	0.03^d
Deer Creek	0.49 ^a	0.29 ^b	0.05^c	0.05^c	0.13^c
West Rocky Creek	0.05^a	0.02^a	0.14 ^b	0.16 ^b	0.64 ^c
Steele Creek	0.46 ^a	0.31 ^b	0.09 ^c	0.09 ^c	0.04^d
Colony Creek	0.16 ^a	0.05^b	0.08^b	0.11 ^a	0.60 ^c
Deadman Creek	0.53 ^a	0.29 ^b	0.05^c	0.05^c	0.09^c
Auds Creek	0.43 ^a	0.30 ^b	0.13 ^c	0.12 ^c	0.02^d
Bluff Creek	0.07 ^a	0.02^b	0.14 ^a	0.13 ^a	0.63 ^c
Wilson Creek	0.18^a	0.06^a	0.06^a	0.10^a	0.60 ^b
Ioni Creek	0.39 ^a	0.17 ^b	0.03^c	0.07 ^b	0.34 ^a
Bluff Creek	0.56 ^a	0.26 ^b	0.04^c	0.08^c	0.07^c
Willis Creek	0.44 ^a	0.29 ^b	0.12 ^c	0.13 ^c	0.02^d
Geronimo Creek	0.28^a	0.11^a	0.07^a	0.06^a	0.48 ^b
Wolf Creek	0.11^a	0.03^a	0.12^a	0.11^a	0.64 ^b
McClellan Creek	0.35 ^a	0.19 ^b	0.11 ^c	0.08^c	0.27 ^a
Whitefish Creek	0.45 ^a	0.27 ^b	0.11 ^c	0.16 ^d	0.01^e
Lelia Lake Creek	0.33 ^a	0.17 ^b	0.13 ^b	0.10^c	0.27 ^a
Saddlers Creek	0.49 ^a	0.20 ^b	0.03^c	0.03^c	0.25 ^a
Devils River	0.44 ^a	0.31 ^b	0.12 ^c	0.12 ^c	0.02^d
Independence Creek	0.46 ^a	0.32 ^b	0.11 ^c	0.10 ^c	0.01^d
Alamito Creek	0.55 ^a	0.30 ^b	0.05^c	0.06^c	0.05^c
Terlingua Creek	0.41 ^a	0.18 ^b	0.04^c	0.02^c	0.35 ^a
Live Oak Creek	0.40 ^a	0.27 ^b	0.14 ^c	0.16 ^d	0.03^e

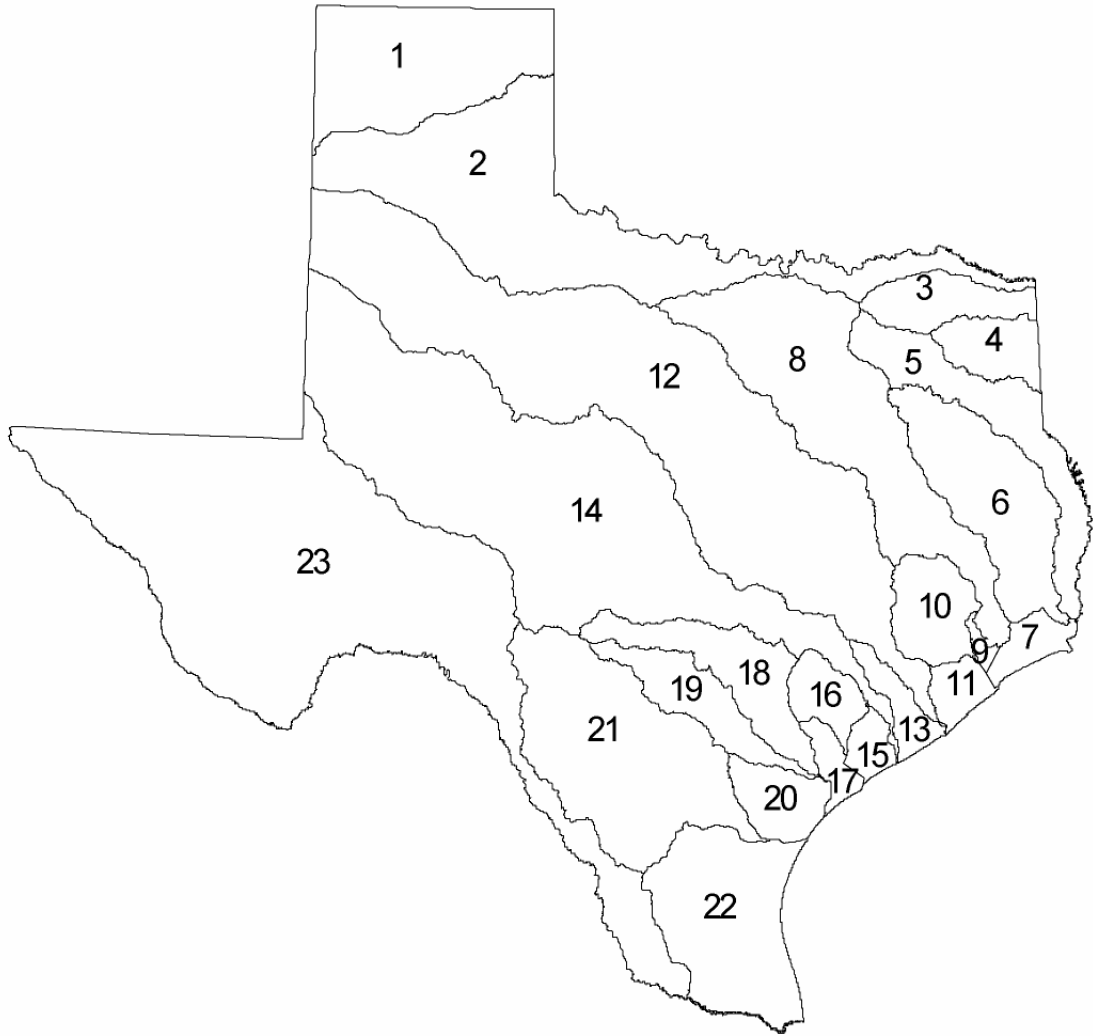


Figure 3.1. River basins of Texas: (1) Canadian, (2) Red, (3) Sulphur, (4) Cypress, (5) Sabine, (6) Neches, (7) Neches-Trinity, (8) Trinity, (9) Trinity-San Jacinto, (10) San Jacinto, (11) San Jacinto-Brazos, (12) Brazos, (13) Brazos-Colorado, (14) Colorado, (15) Colorado-Lavaca, (16) Lavaca, (17) Lavaca-Guadalupe, (18) Guadalupe, (19) San Antonio, (20) San Antonio-Nueces, (21) Nueces, (22) Nueces-Rio Grande, and (23) Rio Grande.

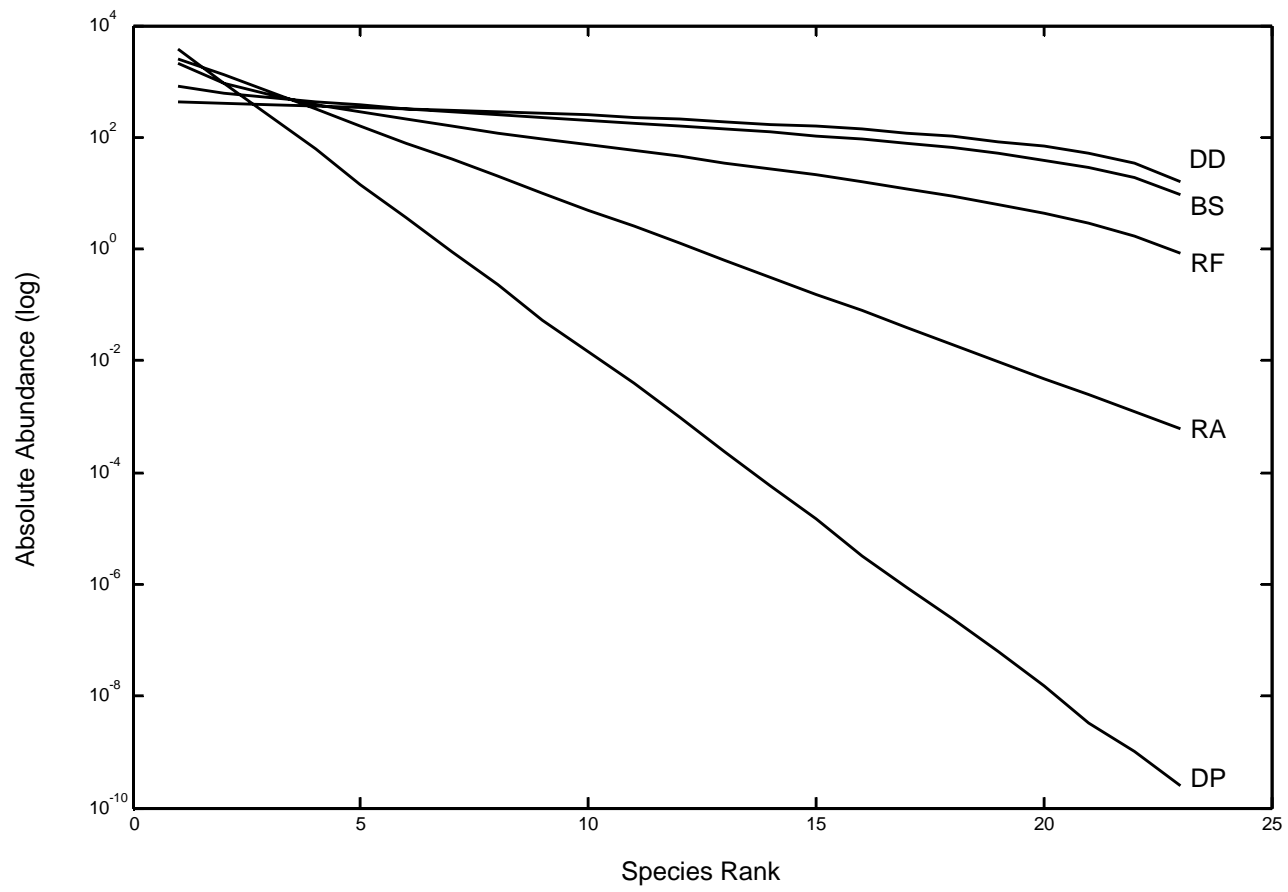


Figure 3.2. Diagrammatic representation of the differences in form among niche partitioning models (dominance decay, DD; brokenstick, BS; random fraction, RF; random assortment, RA; and dominance preemption, DP).

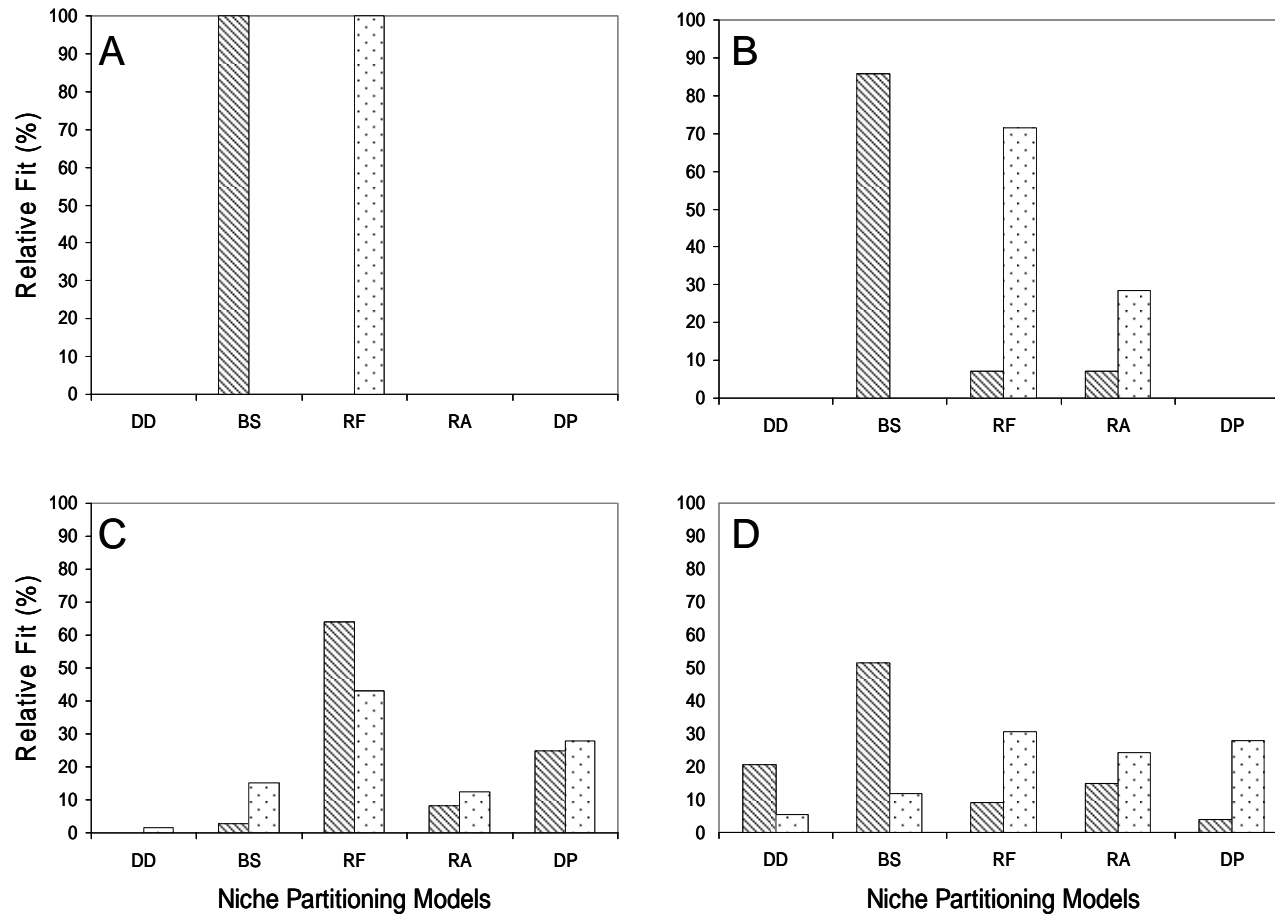


Figure 3.3. Relative fit of niche partitioning models to empirical data across (A) the entire state, (B) ecoregions, (C), river basins, and (D) individual sites. Diagonal hatch corresponds to functional groups and dotted hatch corresponds to species.

CHAPTER IV
SPATIOTEMPORAL VARIATION IN FISH ASSEMBLAGE STRUCTURE BASED
ON FUNCTIONAL GROUPS AND SPECIES COMPOSITION

Abstract

Stream ecosystems across the world are dynamic and complex. Biogeographic and historical constraints cause many of these systems to be unique and create difficulty in predicting compositional changes in fish assemblages. However, each system appears to be comprised of similar functional groupings despite phylogenetic differences. Hence, the objectives of this study were (1) to compare assemblage structure of stream fishes from a taxonomic and functional perspective among rivers and seasons, and (2) to determine whether certain variables that structure taxonomic assemblages (e.g., temperature, current velocity, water depth, substrate, stream width) can be used to predict functional diversity. I surveyed fish assemblages from three tributaries of the Colorado River in Texas (Pedernales River, San Saba River, and South Llano River) across all four seasons and from this data created functional and taxonomic data sets. Fish assemblages within each river were more similar to assemblages from the same river than assemblages from different rivers, regardless of season, from both taxonomic and functional perspectives. However, abiotic variables were better predictors for functional diversity than taxonomic diversity. Such a finding can be very useful for management agencies that are bestowed with the task of helping to maintain freshwater ecosystems.

Introduction

Much of what is known in stream-fish ecology is based on our understanding of patterns and processes associated with the abundance and distribution of species. For example, we know that abiotic (Gorman and Karr 1978; Grossman and Freeman 1987; Ostrand and Wilde 2001; Higgins and Wilde 2005) and biotic (Power and Matthews 1983; Ross 1986; Resetarits 1997; Gilliam and Fraser 2001) determinants are important in structuring stream-fish assemblages, that these determinants may result in assemblages in which species abundance and composition fluctuate through time (Starrett 1951; Grossman et al. 1982; Grossman et al. 1990) or in assemblages in which the same species are found in roughly the same abundance over time (Smith and Powell 1971; Yant et al. 1984; Meffe and Minckley 1987) structured assemblages, and that the physical structure of a stream channel, in concert with flow regimes and energy input, produces a consistent pattern of structure and function along a stream (Vannote et al. 1980; Schlosser 1982; Matthews 1986; Pires et al. 1999; Hoeinghaus et al. 2003). However, trophic structure, a single attribute, is the primary basis for our understanding of the functional organization of stream-fish assemblages. This limits our ability to understand how changes in the diversity of stream fish would affect ecosystem-level processes, which is critical in light of the decrease in biodiversity that is occurring worldwide.

In an attempt to remedy this situation, Poff and Allan (1995) examined the functional organization of fish assemblages in relation to hydrological variability from a multiple-attribute perspective. They analyzed 34 sites in Wisconsin and Minnesota, used clustering methods to identify two functionally similar groups of assemblages, and used

discriminant analysis of hydrological data to predict the two functionally similar groups of assemblages. Poff and Allan based the functional attributes on trophic guild, stream size preference, current velocity preference, substratum preference, tolerance, and body morphology. They found that the hydrological data could discriminate the two groups of assemblages, which were associated with hydrologically variable sites or hydrologically stable sites. Similarly, Goldstein and Meador (2004) examined species functional traits in relation to stream size. They classified 429 freshwater fish from the Mississippi River basin into 29 species-trait categories based on substrate preference, geomorphic preference, trophic ecology, locomotion morphology, reproductive strategy, and stream size preference. They analyzed the relationship between these categories and stream size categories (i.e., small streams, small rivers, medium rivers, large rivers, and variable). Their results suggest differences in habitat structures fish community function and are different for large rivers versus small rivers and streams.

Although the studies by Poff and Allan (1995) and Goldstein and Meador (2004) have contributed greatly to our understanding of the functional organization of stream-fish assemblages, they do not provide information on the temporal nature of functional organization and did not explicitly attempt to predict changes in functional diversity with environmental variables. Therefore, the objectives of this study were (1) to compare assemblage structure of stream fishes from a taxonomic and functional perspective among rivers and seasons, and (2) to determine whether certain variables that structure taxonomic assemblages (e.g., temperature, current velocity, water depth, substrate, stream width) can be used to predict functional diversity. I hypothesized that assemblages

within a river would be more similar to one another, regardless of season, than assemblages from other localities based on taxonomic diversity; however, assemblages from different rivers but within the same season would be more similar to one another based on functional diversity. These hypotheses stem from the assumption that the abundances of individuals within functional groups will be highly correlated with seasonal variation in the energy resources of rivers.

Materials and Methods

Study Area

The Colorado River of Texas is the largest river that lies entirely within state boundaries. It originates in northeastern Dawson County and empties into the Gulf of Mexico at Matagorda Bay, flowing for more than 1,040 km and draining nearly 100,000 km². The five major tributaries of the Colorado River include the Concho, Pecan Bayou, Pedernales, Llano, and San Saba Rivers. With the exception of the Pecan Bayou, the tributaries enter the Colorado River from the west, are spring fed, and arise within the Edwards Plateau region. The Edwards Plateau is the southernmost region of the Great Plains and is characterized by thin soil and limestone bedrock.

The Colorado River supports more than 90 species of freshwater fishes representing 20 families. Three families comprise more than 50% of the species: the Cyprinidae (26 species), Centrarchidae (14 species), and Percidae (10 species). The remaining families represented are Amiidae, Anguillidae, Aphredoderidae, Atherinidae,

Belonidae, Catostomidae, Characidae, Cichlidae, Clupidae, Cyprinodontidae, Esocidae, Ictaluridae, Lepisosteidae, Mugilidae, Perichthyidae, Poeciliidae, and Sciaenidae.

Sampling Methodology

I examined the structure of stream-fish assemblages from three tributaries of the Colorado River (Pedernales River, San Saba River, and South Llano River) on a seasonal basis from April 2003 to February 2004. Each sampling site comprised one 100-meter stretch of stream to provide a representative sample of the ichthyofauna (Matthews 1990). I selected each site so that it was easily accessible and contained as many different geomorphic units (pool, riffle, and run) as possible because these units undoubtedly differ in both biotic and abiotic characteristics. I placed transects every 10 meters and subdivided them into four quadrats corresponding to 0-25% stream width (left-bank), 26-50% stream width (left-center), 51-75% stream width (right-center), and 76-100% stream width (right-bank). I measured several habitat characteristics in three random locations for each section; the variables measured or scored were temperature (°C), water depth (cm), water velocity at the middle of the water column (m/s), dominant substrate type (i.e., smooth, gravel, cobble, boulder, bedrock), and habitat type (pool, riffle, run). In addition, I used backpack electrofishing to inventory the fishes at each site. I sampled each quadrat of each transect thoroughly for three minutes. I placed the captured fishes from each of the quadrats in separate five-gallon buckets containing MS-222. After sampling the entire stream reach, I placed the euthanized fishes in 10% formalin to harden the tissues and to preserve the individuals until returning to the lab,

where I stored them in 70% ethanol. All of the above procedures were approved beforehand by the Animal Care and Use Committee of Texas Tech University (ACUC # 04031-07) and the Texas Parks and Wildlife Department (Scientific Permit # SPR-0403-284).

Formation of Functional Groups

To classify fish species into functional groups, I used a classification scheme proposed by William Matthews (1998) that emphasizes the organism's role in ecosystem processes. This classification scheme expanded traditional trophic groups (e.g., herbivore, piscivore, invertivore) to include the manner in which fishes affect aquatic ecosystems. Although this classification scheme has not been inspected for its general usefulness nor have the groups been tested for differences in ecosystem level processes (e.g., nutrient cycling), it provides an initial framework to examine patterns of functional diversity in stream fishes by examining what fish eat, where they find food, and how they consume resources (Matthews 1998). This classification scheme imposes an important distinction between fishes that physically disturb substrates from fishes that do not disturb substrates, which should differentially affect ecosystem processes such as nutrient cycling. In addition to this dichotomy, Matthews incorporated information on the manner in which fishes feed. For example he distinguished suction piscivores from biting piscivores because suction piscivores generally swallow prey whole, whereas biting piscivores tend to leave fragments in the environment that other organisms can consume. Hence, this classification scheme is specifically designed to directly address

issues regarding ecosystem function, whether it is aspects of decomposition, primary production, nutrient cycling, or energy flow.

The specific functional groups I used in this study were (1) grazers, (2) browsers, (3) benthic detritivores, (4) mud or sand sifter, (5) disturbance pickers, (6) scavengers, (7) egg eaters, (8) filter feeders, (9) surface feeders, (10) water-column particulate feeders, (11) benthic pickers, (12) snail crushers, (13) suction piscivores, and (14) biting piscivores. Grazers scrape materials (e.g., algae) from hard substrates such as rocks and woody debris. Browsers feed on plant materials that are suspended in the water column, directly affecting primary productivity. Benthic detritivores consume dead or decaying matter from the bottom of aquatic environments, thereby physically disturbing the substrate. Mud or sand sifters consume soft sediments to sift out invertebrate food items, increasing the suspension of fine particulate organic matter. Disturbance pickers mechanically disturb substrates in order to feed on invertebrate prey while increasing the suspension of fine particulate organic matter. Scavengers feed on a variety of animal material, dead or alive, directly altering energy flow. Egg eaters consume eggs of other fishes, directly affecting the abundance of other functional groups. Filter feeders remove micro-organisms from the water column, which directly impacts primary productivity and prey availability for other drift feeding fishes. Surface feeders consume invertebrates from the top of the water column, thereby indirectly affecting the abundance of phytoplankton that many invertebrates feed on in turn affecting primary productivity. Water column particulate feeders feed on invertebrates in the middle of the water column. Benthic pickers do not disturb the substrate like disturbance pickers, but they do consume

inveterate from the benthos. Snail crushers consume hard bodied invertebrates, such as snails and crayfish. Suction piscivores consume other fishes by swallowing prey whole, leaving no fragments for other organisms to consume. Biting piscivores, on the other hand, are messy eaters and leave fragments of fish in the environment.

I assigned fish species to as many functional groups as needed based on accounts in the literature that documented feeding habits, reproductive strategies, or habitat requirements (Appendix A). I classified many species into multiple functional groups to reflect their opportunistic feeding strategies and ontogenetic shifts in diet. For these fishes, I partitioned the total number of individuals equally into the multiple functional groups so as not to artificially inflate the ecological importance of generalist species. Species that belonged to only one functional group had all individuals placed into that group.

Indices of Diversity

I estimated several ecological indices of assemblage structure, including species richness (S), Shannon diversity (H), Camargo evenness (E), and Berger-Parker dominance (D) because they characterize different aspects of community structure (Stevens and Willig 2002; Magurran 2004). I estimated species richness by simply determining the number of species collected at each locality. I calculated Shannon diversity as $H = -\sum p_i \ln p_i$, which simultaneously accounted for richness and evenness (Pielou 1975). I calculated Camargo evenness (Camargo 1995),

$$E = 1 - \left(\sum_{i=1}^S \sum_{j=i+1}^S \left[\frac{P_i - P_j}{S} \right] \right),$$

which measures the equability of species abundances within a particular locality. Camargo evenness values range from 0, which characterizes an assemblage in which species abundances differ greatly, to 1, which characterizes an assemblage in which species are equally abundant. Berger-Parker dominance (Berger and Parker 1970), $D = N_{\max}/N$, assesses the degree to which assemblage structure is dominated by the most abundant species. I inverted the Berger-Parker index values so that larger values represent lower dominance, or increased biodiversity (Magurran 2004).

Similarity Index

I made comparisons of assemblage structure using the Bray-Curtis index of similarity (Bray and Curtis 1957), which is sometimes called the Sorensen quantitative index (Magurran 2004). The Bray-Curtis index is one of many similarity measures, but I used it in this study because it has been found to meet certain criteria that other measures do not, including the fact that it is based on total abundances rather than relative abundances (Clarke and Warwick 2001). I calculated the Bray-Curtis index using the formula $C_{BC} = \frac{2jN}{N_a + N_b}$ where N_a is the total number of individuals at site A, N_b is the total number of individuals at site B, and $2jN$ is the sum of the lower of the two abundances for species found at both sites across species (Magurran 2004). C_{BC} ranges from 0, when assemblages have no species in common, to 1 when assemblages are identical; thus, one can interpret the Bray-Curtis index as percent similarity between two

assemblages. Similarity indices were estimated using MATLAB v 6.0 software (Mathworks 1997).

Multivariate Analyses

I used detrended canonical correspondence analysis (DCCA; MVSP for Windows, Version 3) on abundance data with a downweighting of the rare species (those that occurred at fewer than 20% of the number of sites occupied by the most common species) to characterize patterns of variation in taxonomic and functional diversity among stream-fish assemblages (Hill and Gauch 1980). Downweighting is a method that decreases the importance of rare species in proportion to the most common species, which should provide a more robust assessment by emphasizing abundant species. I chose DCCA over detrended correspondence analysis (Ter Braak 1986; Palmer 2002) because it provides a direct assessment of the effects of environmental factors on patterns of variation in abundance by using nonlinear regression techniques rather than simple linear correlations. These analyses provide a slightly different approach to confront my hypotheses than just analyzing indices of diversity, by incorporating environmental factors into the analyses.

I used partial least squares (PLS) regression to formulate predictive models of functional diversity based on environmental variables (i.e., stream width, temperature, water depth, current velocity, and substrate). PLS is a less restrictive extension of the multiple linear regression model that is used when many factors (i.e., independent variables) and response variables (i.e., dependent variables) are involved, when factors or

response variables are correlated, or when the relationship between factors and response variables are not well-understood (Geladi and Kowalski 1986). However, disadvantages exist with PLS. These include greater difficulty in interpreting the results and an inability to assess statistical significance without utilizing a randomization procedure such as the bootstrap (Tobias 1997). Consequently, I used the predicted residual sum of squares with cross-validation as the test statistic. The number of latent variables (linear relationships between factors and response variables) extracted was chosen corresponded with the minimum prediction error on the validation set.

Results

A total of 4,948 fish representing 24 species in seven families was collected across all four seasons and three localities. I collected a total of 20 species in the Pedernales River (Table 4.1), 19 species in the San Saba River (Table 4.2), and 21 species in the South Llano River (Table 4.3). The Pedernales River fauna primarily consisted of mosquitofish *Gambusia affinis*, blacktail shiner *Cyprinella venusta*, bluegill sunfish *Lepomis macrochirus*, and longear sunfish *L. megalotis*. The San Saba River fauna consisted primarily of blacktail shiner, mosquitofish, mimic shiner *Notropis volucellus*, longear sunfish, and bluegill sunfish. The South Llano River fauna primarily consisted of roundnose minnow *Dionda episcopa*, greenthroat darters *Etheostoma lepidum*, orangethroat darters *E. spectabile*, and Rio Grande cichlids *Cichlasoma cyanoguttatum*. I observed 11 functional groups in the Pedernales River (Table 4.4), San Saba River (Table 4.5), and South Llano River (Table 4.6). The Pedernales River fauna

consisted primarily of surface feeders and egg eaters. The San Saba River fauna consisted primarily of water column particulate feeders and benthic pickers. The South Llano River fauna, on the other hand, consisted primarily of browsers and benthic pickers. Accumulation curves suggested that maximal functional richness was achieved with the sampling scheme implemented, whereas taxonomic richness may have been slightly underestimated in spring and summer for the Pedernales River, summer for the San Saba River, and spring and summer for the South Llano River (Figure 4.1).

Based on Bray-Curtis indices, fish assemblages within each river were more similar to assemblages from the same river than assemblages from different rivers, regardless of season, from both taxonomic (Table 4.7) and functional (Table 4.8) perspectives. I observed the same pattern when environmental variables were incorporated into direct ordination methods, for DCCA resulted in assemblages from the same river, regardless of season, clustering together (Figure 4.2). I observed this pattern both for species composition and for functional groups. Functional and taxonomic differences in assemblage structure among rivers and seasons were idiosyncratic from the perspectives of richness (Figure 4.3), diversity (Figure 4.4), evenness (Figure 4.5), and dominance (Figure 4.6), with no clear patterns emerging.

Partial least squares regression accounted for 50.8% of the variation in functional diversity (Table 4.9) and 42.1% of the variation in taxonomic diversity (Table 4.10). Four linear combinations were extracted that accounted for a significant amount of the variation in functional diversity (35.3%, 5.7%, 3.5%, and 6.2% respectively). Water depth and current velocity were the major environmental variables that contributed to

first and fourth extracted factors. Temperature contributed most to the second extracted factor. Stream width and substrate contributed more to the third extracted factor than the other environmental variables. Two linear combinations were extracted that accounted for a significant amount of the variation in taxonomic diversity (25.8% and 16.3% respectively). Stream width and substrate were the major environmental variables that contributed to the first extracted factor. Temperature and current velocity were important in structuring the second extracted factor.

Discussion

Stream ecosystems are dependent on two types of energy input: autochthonous and allochthonous energy production. Autochthonous energy is produced within the stream channel by photosynthetic organisms living within the stream, such as microscopic algae, cyanobacteria, and macrophytes (e.g., mosses and liverworts). Algae and cyanobacteria directly contribute more energy to heterotrophs than do macrophytes, which are mostly unpalatable. However, macrophytes do contribute to the production of dissolved organic matter and particulate organic matter. Allochthonous energy, on the other hand, is produced outside the stream (e.g., leaves, fruit, twigs, or logs) and falls or leaches into the stream channel. The amount of autochthonous and allochthonous energy within a stream is highly dependent on seasonal variation in temperature, sunlight, and precipitation (Vannote et al. 1980). Despite this seasonal variation in energy availability within a stream, the hypothesis that the functional organization of stream fish will cause

assemblages from different localities to be more similar to one another within a season than assemblages from the same locality through time was not supported by the data.

This finding suggests either that changes in abundance within functional groups were not coincident with seasonal variation in energy input or that seasonal changes in environmental conditions among the three rivers were not great enough to influence fish abundances. Although central Texas does not have pronounced seasonality, it is more likely that abundance within functional groups did not change in response to seasonal variations. No matter how species are classified, whether into trophic guilds (Schlosser 1982; Flecker 1992; Jepsen and Winemiller 2002), habitat guilds (Schlosser 1982; Leonard and Orth 1988; Vadas and Orth 2001), reproductive guilds (Balon 1975; Jones et al. 1999; Growns 2004), or functional groups (Matthews 1998; Goldstein and Meador 2004), it is the individuals that are responding to environmental conditions rather than the groups themselves. These individuals are faced with the daunting task of surviving and reproducing, even in the harshest of conditions. Through the process of natural selection, many species of fish time their spawning activities such that larval stages enter the environment at the same time there is a spike in the abundance of phytoplankton, which typically occurs in the spring (Hjort 1914; Cushing 1978; Platt et al. 2003). This results in fairly uniform changes in relative abundances among species through time. Consequently, relative abundances within functional groups should also be rather consistent among groups. These similarities in changes in abundances among functional groups would lead to a similar organization between taxonomic and functional aspects of stream-fish assemblages.

Although assemblage structure was not noticeably different from a functional versus taxonomic standpoint, results suggest that environmental variables (i.e., stream width, water temperature, water depth, current velocity, and substrate) can be used to predict changes in local biodiversity more precisely for functional diversity than taxonomic diversity. Water depth and current velocity were the primary factors accounting for changes in functional diversity. Both of these factors have been shown to be very influential in structuring stream fish assemblages from a traditional taxonomic point of view (Mendelson 1975; Baker and Ross 1981; Schlosser 1985). Surprisingly, depth and velocity were not the major factors accounting for changes in taxonomic diversity; rather, stream width and substrate type were the primary factors. Substrate type, however, has been shown to an important component of the habitat that structures stream-fish assemblages (e.g., Gorman and Karr 1978).

The results of this study are complementary to the studies conducted by Poff and Allan (1995) and Goldstein and Meador (2004). All three studies suggest that the functional organization of stream-fish assemblages is strongly associated with environmental variables, which provides strong evidence that functional diversity and species traits can be predicted from certain abiotic covariates of biodiversity. Such a finding can be very useful for management agencies that are bestowed with the task of helping to maintain freshwater ecosystems. Many pristine systems are becoming increasingly modified through anthropogenic activities. These modifications can interrupt the interactions among constituent biota and even threaten the survival of freshwater ecosystems. Often, a single event can have both direct and indirect effects on

the ecosystem. For example, the removal of riparian vegetation (1) causes river bank erosion, which leads to altered flow patterns and sedimentation; (2) results in less woody debris in rivers, decreasing habitat availability for aquatic organisms; and (3) increases water temperatures due to the lack of shade. By understanding how functional diversity can change with the abiotic environment, agencies can attempt to manage the environmental conditions so that functional diversity is maximized.

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Table. 4.1. Seasonal variation in abundance of fish species collected in the Pedernales River between 2003 and 2004.

Species	Common Name	Spring	Summer	Fall	Winter
<i>Ameiurus natalis</i>	Yellow bullhead	0	0	0	0
<i>Campostoma anomalum</i>	Central stoneroller	0	0	0	2
<i>Carpiodes carpio</i>	River carpsucker	0	0	1	0
<i>Cichlasoma cyanoguttatum</i>	Rio Grande cichlid	0	0	0	0
<i>Cyprinella venusta</i>	Blacktail shiner	43	14	77	19
<i>Dionda episcopa</i>	Roundnose minnow	0	0	20	0
<i>Etheostoma lepidum</i>	Greenthroat darter	3	0	13	3
<i>Etheostoma spectabile</i>	Orangethroat darter	1	0	0	0
<i>Gambusia affinis</i>	Mosquitofish	29	7	187	107
<i>Ictalurus punctatus</i>	Channel catfish	1	1	2	1
<i>Lepomis auritus</i>	Redbreast sunfish	9	0	96	38
<i>Lepomis cyanellus</i>	Green sunfish	13	1	47	15
<i>Lepomis gulosus</i>	Warmouth sunfish	1	1	1	0
<i>Lepomis macrochirus</i>	Bluegill sunfish	2	4	121	17
<i>Lepomis megalotis</i>	Longear sunfish	13	4	72	31
<i>Micropterus dolomieu</i>	Smallmouth bass	0	0	0	0
<i>Micropterus punctatus</i>	Spotted bass	0	0	7	3
<i>Micropterus salmoides</i>	Largemouth bass	0	0	1	0
<i>Moxostoma congestum</i>	Gray redhorse	2	0	9	0
<i>Notropis amabilis</i>	Texas shiner	0	0	0	0
<i>Notropis volucellus</i>	Mimic shiner	1	10	75	8
<i>Percina carbonaria</i>	Texas logperch	6	0	14	2
<i>Pimephales vigilax</i>	Bullhead minnow	0	4	36	0
<i>Pylodictis olivaris</i>	Flathead catfish	0	1	0	0
Total		124	47	779	246

Table. 4.2. Seasonal variation in abundance of fish species collected in the San Saba River between 2003 and 2004.

Species	Common Name	Spring	Summer	Fall	Winter
<i>Ameiurus natalis</i>	Yellow bullhead	0	0	0	0
<i>Campostoma anomalum</i>	Central stoneroller	0	51	6	5
<i>Carpiodes carpio</i>	River carpsucker	0	0	0	0
<i>Cichlasoma cyanoguttatum</i>	Rio Grande cichlid	0	0	0	0
<i>Cyprinella venusta</i>	Blacktail shiner	529	177	241	185
<i>Dionda episcopa</i>	Roundnose minnow	20	0	0	0
<i>Etheostoma lepidum</i>	Greenthroat darter	7	2	10	19
<i>Etheostoma spectabile</i>	Orangethroat darter	1	0	12	11
<i>Gambusia affinis</i>	Mosquitofish	109	87	55	10
<i>Ictalurus punctatus</i>	Channel catfish	0	8	2	0
<i>Lepomis auritus</i>	Redbreast sunfish	21	6	17	12
<i>Lepomis cyanellus</i>	Green sunfish	0	6	9	10
<i>Lepomis gulosus</i>	Warmouth sunfish	0	0	0	0
<i>Lepomis macrochirus</i>	Bluegill sunfish	10	10	74	23
<i>Lepomis megalotis</i>	Longear sunfish	27	11	85	35
<i>Micropterus dolomieu</i>	Smallmouth bass	0	0	0	0
<i>Micropterus punctatus</i>	Spotted bass	0	8	17	12
<i>Micropterus salmoides</i>	Largemouth bass	0	1	0	0
<i>Moxostoma congestum</i>	Gray redhorse	0	1	2	0
<i>Notropis amabilis</i>	Texas shiner	31	0	2	6
<i>Notropis volucellus</i>	Mimic shiner	195	3	25	18
<i>Percina carbonaria</i>	Texas logperch	7	0	12	16
<i>Pimephales vigilax</i>	Bullhead minnow	24	0	0	1
<i>Pylodictis olivaris</i>	Flathead catfish	0	1	0	0
Total		981	372	569	363

Table. 4.3. Seasonal variation in abundance of fish species collected in the South Llano River between 2003 and 2004.

Species	Common Name	Spring	Summer	Fall	Winter
<i>Ameiurus natalis</i>	Yellow bullhead	1	0	0	0
<i>Campostoma anomalum</i>	Central stoneroller	0	9	31	5
<i>Carpiodes carpio</i>	River carpsucker	0	0	0	0
<i>Cichlasoma cyanoguttatum</i>	Rio Grande cichlid	1	29	61	15
<i>Cyprinella venusta</i>	Blacktail shiner	6	1	26	11
<i>Dionda episcopa</i>	Roundnose minnow	121	58	212	52
<i>Etheostoma lepidum</i>	Greenthroat darter	51	36	74	147
<i>Etheostoma spectabile</i>	Orangethroat darter	38	28	79	36
<i>Gambusia affinis</i>	Mosquitofish	5	5	53	7
<i>Ictalurus punctatus</i>	Channel catfish	4	1	7	5
<i>Lepomis auritus</i>	Redbreast sunfish	6	1	13	24
<i>Lepomis cyanellus</i>	Green sunfish	5	0	12	16
<i>Lepomis gulosus</i>	Warmouth sunfish	3	0	0	0
<i>Lepomis macrochirus</i>	Bluegill sunfish	11	0	12	9
<i>Lepomis megalotis</i>	Longear sunfish	15	2	13	6
<i>Micropterus dolomieu</i>	Smallmouth bass	0	1	0	0
<i>Micropterus punctatus</i>	Spotted bass	0	2	0	0
<i>Micropterus salmoides</i>	Largemouth bass	0	0	0	0
<i>Moxostoma congestum</i>	Gray redhorse	0	0	8	1
<i>Notropis amabilis</i>	Texas shiner	24	0	5	17
<i>Notropis volucellus</i>	Mimic shiner	1	2	0	6
<i>Percina carbonaria</i>	Texas logperch	2	0	28	6
<i>Pimephales vigilax</i>	Bullhead minnow	0	0	0	0
<i>Pylodictis olivaris</i>	Flathead catfish	0	1	0	0
Total		294	176	634	363

Table. 4.4. Seasonal variation in abundance of functional groups collected in the Pedernales River between 2003 and 2004.

Functional Group	Spring	Summer	Fall	Winter
Benthic detritivores	15	9	63	8
Benthic pickers	20	10	79	10
Browsers	1	0	24	1
Disturbance pickers	3	0	7	1
Egg eaters	19	6	142	66
Grazers	1	0	5	3
Scavenges	1	1	1	1
Snail crushers	3	0	29	10
Suction piscivores	11	4	93	29
Surface feeders	25	9	201	82
Water column particulate feeders	25	10	136	36

Table. 4.5. Seasonal variation in abundance of functional groups collected in the San Saba River between 2003 and 2004.

Functional Group	Spring	Summer	Fall	Winter
Benthic detritivores	237	60	87	67
Benthic pickers	254	61	104	89
Browsers	22	1	3	6
Disturbance pickers	4	0	6	8
Egg eaters	64	49	73	25
Grazers	2	52	9	11
Scavenges	0	4	1	0
Snail crushers	5	3	5	3
Suction piscivores	15	17	57	27
Surface feeders	128	53	81	32
Water column particulate feeders	250	73	143	95

Table. 4.6. Seasonal variation in abundance of functional groups collected in the South Llano River between 2003 and 2004.

Functional Group	Spring	Summer	Fall	Winter
Benthic detritivores	3	8	24	9
Benthic pickers	48	34	108	85
Browsers	138	70	237	101
Disturbance pickers	1	0	14	3
Egg eaters	28	17	72	25
Grazers	17	21	56	54
Scavenges	2	1	4	3
Snail crushers	2	8	23	10
Suction piscivores	13	3	17	18
Surface feeders	21	4	42	26
Water column particulate feeders	21	10	39	30

Table 4.7. Bray-Curtis index values of spatiotemporal similarity between assemblages based on species composition and corresponding confidence intervals. Lower confidence limits are below and upper limits are above the diagonal.

Indices	South Llano River				San Saba River				Pedernales River				
	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter	
SLR	Spring	1.000	0.570	0.578	0.612	0.152	0.150	0.178	0.265	0.220	0.135	0.162	0.204
	Summer	0.570	1.000	0.420	0.549	0.067	0.095	0.113	0.178	0.100	0.108	0.098	0.090
	Fall	0.578	0.420	1.000	0.516	0.192	0.304	0.286	0.279	0.274	0.091	0.263	0.295
	Winter	0.612	0.549	0.516	1.000	0.165	0.166	0.221	0.298	0.251	0.166	0.212	0.282
SSR	Spring	0.152	0.067	0.192	0.165	1.000	0.438	0.506	0.423	0.194	0.084	0.428	0.321
	Summer	0.150	0.095	0.304	0.166	0.438	1.000	0.610	0.648	0.411	0.167	0.370	0.485
	Fall	0.178	0.113	0.286	0.221	0.506	0.610	1.000	0.738	0.343	0.133	0.537	0.410
	Winter	0.265	0.178	0.279	0.298	0.423	0.648	0.738	1.000	0.402	0.200	0.385	0.384
PR	Spring	0.220	0.100	0.274	0.251	0.194	0.411	0.343	0.402	1.000	0.363	0.272	0.497
	Summer	0.135	0.108	0.091	0.166	0.084	0.167	0.133	0.200	0.363	1.000	0.111	0.266
	Fall	0.162	0.098	0.263	0.212	0.428	0.370	0.537	0.385	0.272	0.111	1.000	0.476
	Winter	0.204	0.090	0.295	0.282	0.321	0.485	0.410	0.384	0.497	0.266	0.476	1.000
Confidence Intervals													
SLR	Spring	0.000	0.609	0.597	0.661	0.177	0.174	0.218	0.317	0.263	0.182	0.196	0.252
	Summer	0.506	0.000	0.430	0.597	0.088	0.128	0.145	0.226	0.140	0.143	0.124	0.123
	Fall	0.541	0.407	0.000	0.562	0.219	0.340	0.313	0.315	0.303	0.109	0.300	0.336
	Winter	0.530	0.475	0.461	0.000	0.188	0.196	0.255	0.344	0.296	0.195	0.247	0.322
SSR	Spring	0.125	0.047	0.165	0.134	0.000	0.458	0.538	0.451	0.205	0.089	0.465	0.342
	Summer	0.102	0.062	0.256	0.120	0.411	0.000	0.657	0.688	0.452	0.196	0.410	0.547
	Fall	0.141	0.081	0.243	0.180	0.470	0.559	0.000	0.755	0.355	0.146	0.576	0.461
	Winter	0.216	0.130	0.229	0.242	0.390	0.588	0.689	0.000	0.448	0.220	0.424	0.430
PR	Spring	0.158	0.047	0.224	0.185	0.174	0.347	0.312	0.345	0.000	0.433	0.275	0.562
	Summer	0.082	0.045	0.070	0.107	0.074	0.129	0.114	0.166	0.269	0.000	0.114	0.294
	Fall	0.132	0.071	0.226	0.179	0.386	0.325	0.487	0.340	0.264	0.102	0.000	0.480
	Winter	0.152	0.047	0.248	0.220	0.279	0.417	0.356	0.319	0.411	0.198	0.468	0.000

Table 4.8. Bray-Curtis index values of spatiotemporal similarity between assemblages based on functional groups and corresponding confidence intervals. Lower confidence limits are below and upper limits are above the diagonal.

Indices	South Llano River				San Saba River				Pedernales River				
	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter	
SLR	Spring	1.000	0.685	0.632	0.772	0.253	0.468	0.348	0.460	0.483	0.251	0.311	0.384
	Summer	0.685	1.000	0.433	0.652	0.182	0.372	0.252	0.356	0.453	0.373	0.238	0.307
	Fall	0.632	0.433	1.000	0.726	0.402	0.579	0.534	0.509	0.326	0.143	0.470	0.442
	Winter	0.772	0.652	0.726	1.000	0.330	0.616	0.459	0.594	0.484	0.237	0.402	0.435
SSR	Spring	0.253	0.182	0.402	0.330	1.000	0.468	0.655	0.503	0.223	0.093	0.588	0.365
	Summer	0.468	0.372	0.579	0.616	0.468	1.000	0.694	0.769	0.487	0.232	0.560	0.584
	Fall	0.348	0.252	0.534	0.459	0.655	0.694	1.000	0.764	0.358	0.159	0.755	0.591
	Winter	0.460	0.356	0.509	0.594	0.503	0.769	0.764	1.000	0.505	0.233	0.598	0.479
PR	Spring	0.483	0.453	0.326	0.484	0.223	0.487	0.358	0.505	1.000	0.566	0.274	0.566
	Summer	0.251	0.373	0.143	0.237	0.093	0.232	0.159	0.233	0.566	1.000	0.118	0.324
	Fall	0.311	0.238	0.470	0.402	0.588	0.560	0.755	0.598	0.274	0.118	1.000	0.481
	Winter	0.384	0.307	0.442	0.435	0.365	0.584	0.591	0.479	0.566	0.324	0.481	1.000
Confidence Intervals													
SLR	Spring	0.000	0.728	0.632	0.830	0.281	0.510	0.389	0.511	0.522	0.286	0.348	0.444
	Summer	0.626	0.000	0.433	0.652	0.209	0.423	0.290	0.412	0.533	0.409	0.274	0.359
	Fall	0.617	0.431	0.000	0.728	0.432	0.616	0.563	0.555	0.326	0.143	0.510	0.480
	Winter	0.690	0.615	0.680	0.000	0.361	0.662	0.499	0.627	0.504	0.237	0.434	0.478
SSR	Spring	0.221	0.156	0.364	0.296	0.000	0.486	0.681	0.522	0.224	0.095	0.626	0.384
	Summer	0.414	0.324	0.517	0.540	0.443	0.000	0.726	0.823	0.495	0.232	0.581	0.652
	Fall	0.306	0.212	0.478	0.412	0.619	0.662	0.000	0.777	0.358	0.159	0.793	0.603
	Winter	0.399	0.304	0.458	0.520	0.479	0.701	0.730	0.000	0.509	0.238	0.625	0.534
PR	Spring	0.402	0.360	0.311	0.410	0.208	0.455	0.343	0.468	0.000	0.566	0.274	0.625
	Summer	0.216	0.267	0.140	0.199	0.089	0.227	0.149	0.223	0.520	0.000	0.118	0.331
	Fall	0.274	0.201	0.428	0.360	0.544	0.522	0.703	0.548	0.265	0.111	0.000	0.481
	Winter	0.325	0.236	0.387	0.360	0.327	0.516	0.529	0.407	0.485	0.250	0.471	0.000

Table 4.9. Partial least-squares (PLS) regression analysis of functional diversity, with cross-validation.

Number of PLS factors	Percent variation accounted for				Cross-validation	
	Factors		Response		T2	P
	Current	Total	Current	Total		
0					9.33	0.005
1	26.1	26.10	35.3	35.3	8.65	0.020
2	32.44	58.54	5.72	41.02	7.43	0.068
3	30.9	89.44	3.53	44.55	9.28	0.014
4	9.79	99.23	6.22	50.77	0	1.000
5	0.77	100.00	7.45	58.52	7.67	0.042

Table 4.10. Partial least-squares (PLS) regression analysis of taxonomic diversity, with cross-validation.

Number of PLS factors	Percent variation accounted for				Cross- validation	
	Factors		Response		T2	P
	Current	Total	Current	Total		
0					8.35	0.005
1	46.24	46.24	25.8	25.8	9.23	0.006
2	24.52	70.76	16.26	42.06	0.00	1.000
3	9.13	79.89	10.56	52.62	8.38	0.009
4	19.18	99.07	1.14	53.76	8.08	0.011
5	0.93	10.00	7.67	61.43	9.57	0.012

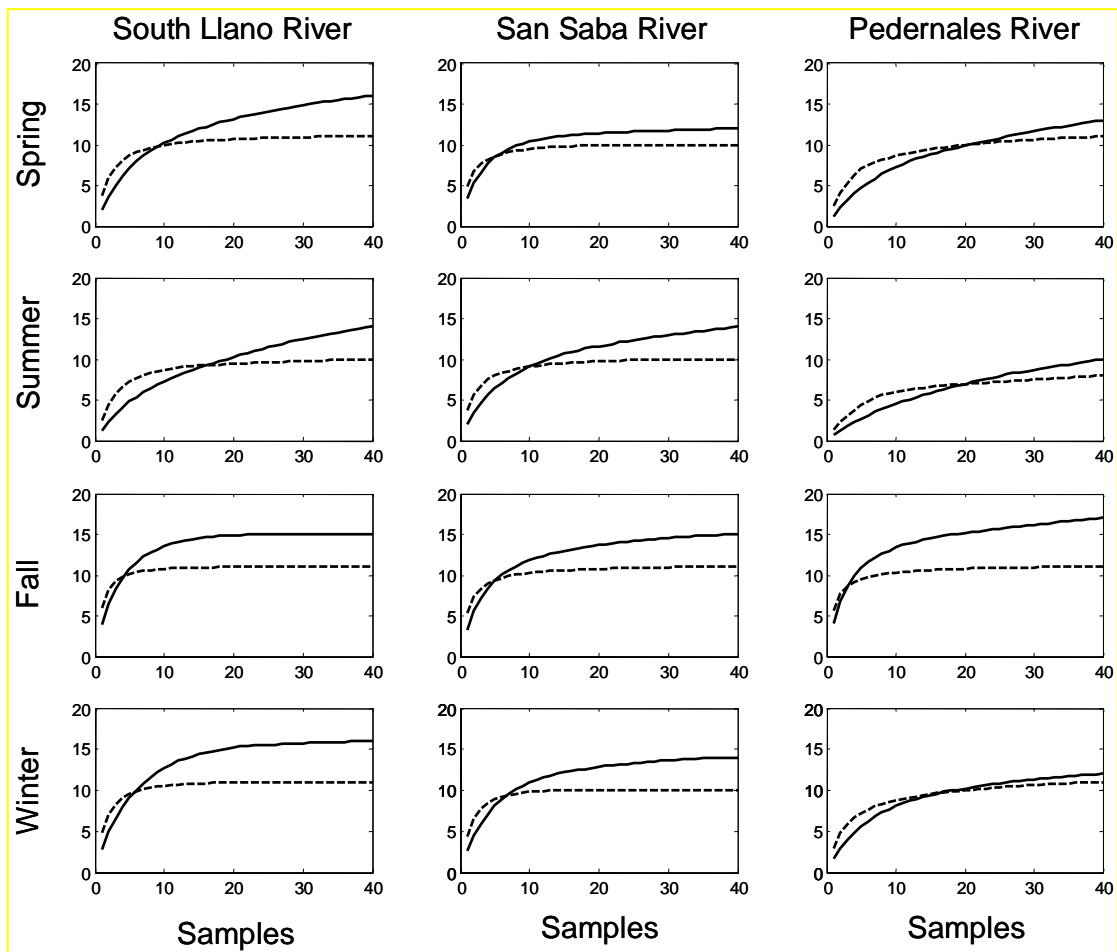


Figure 4.1. Accumulation curves for functional richness (dashed line) and taxonomic richness (solid line) for location and season.

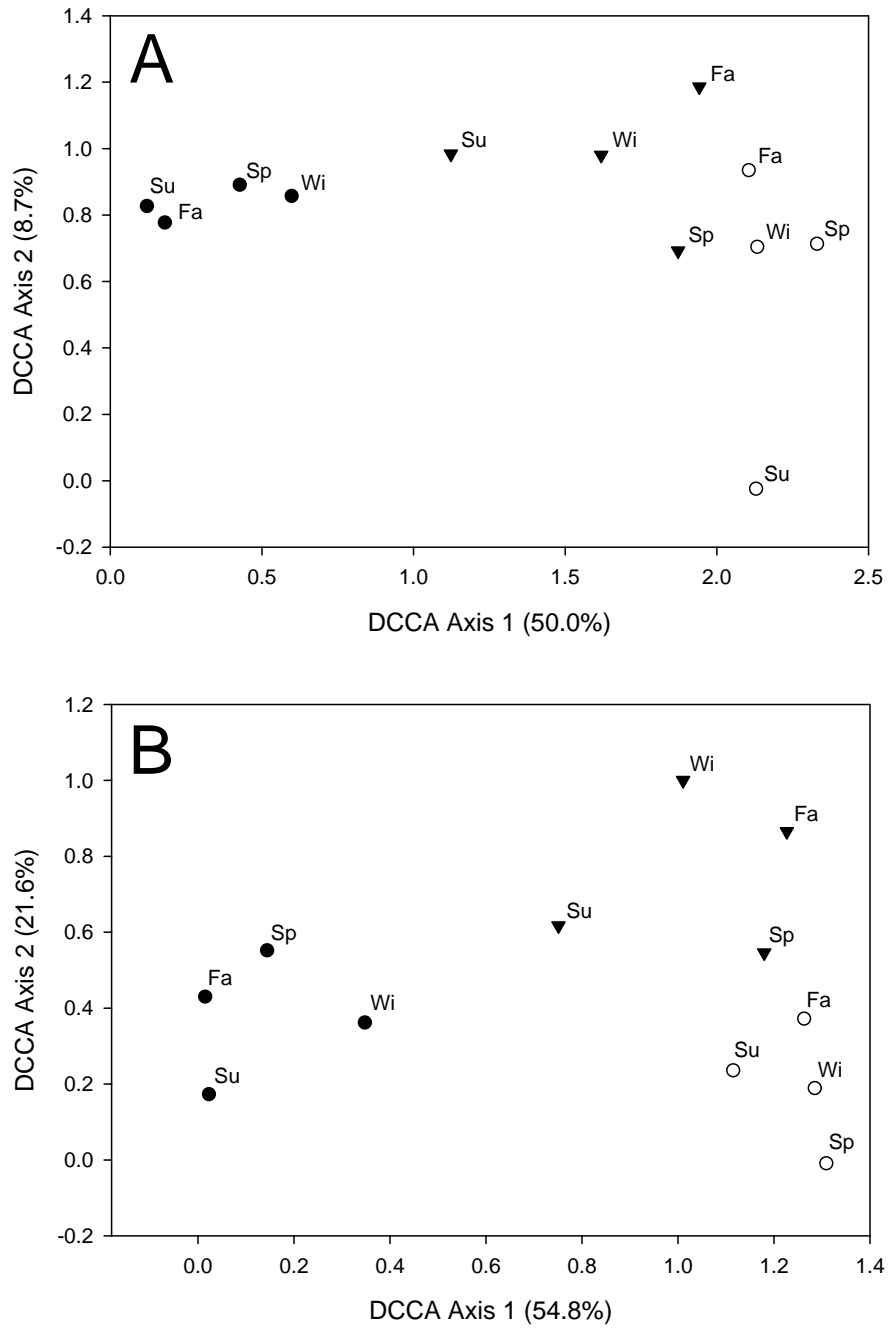


Figure 4.2. Plot of the first and second axis scores from DCCA of Colorado River tributaries from a (A) taxonomic and (B) functional perspective. Triangles represent the Pedernales River. Open circles represent the San Saba River. Closed circles represent the South Llano River.

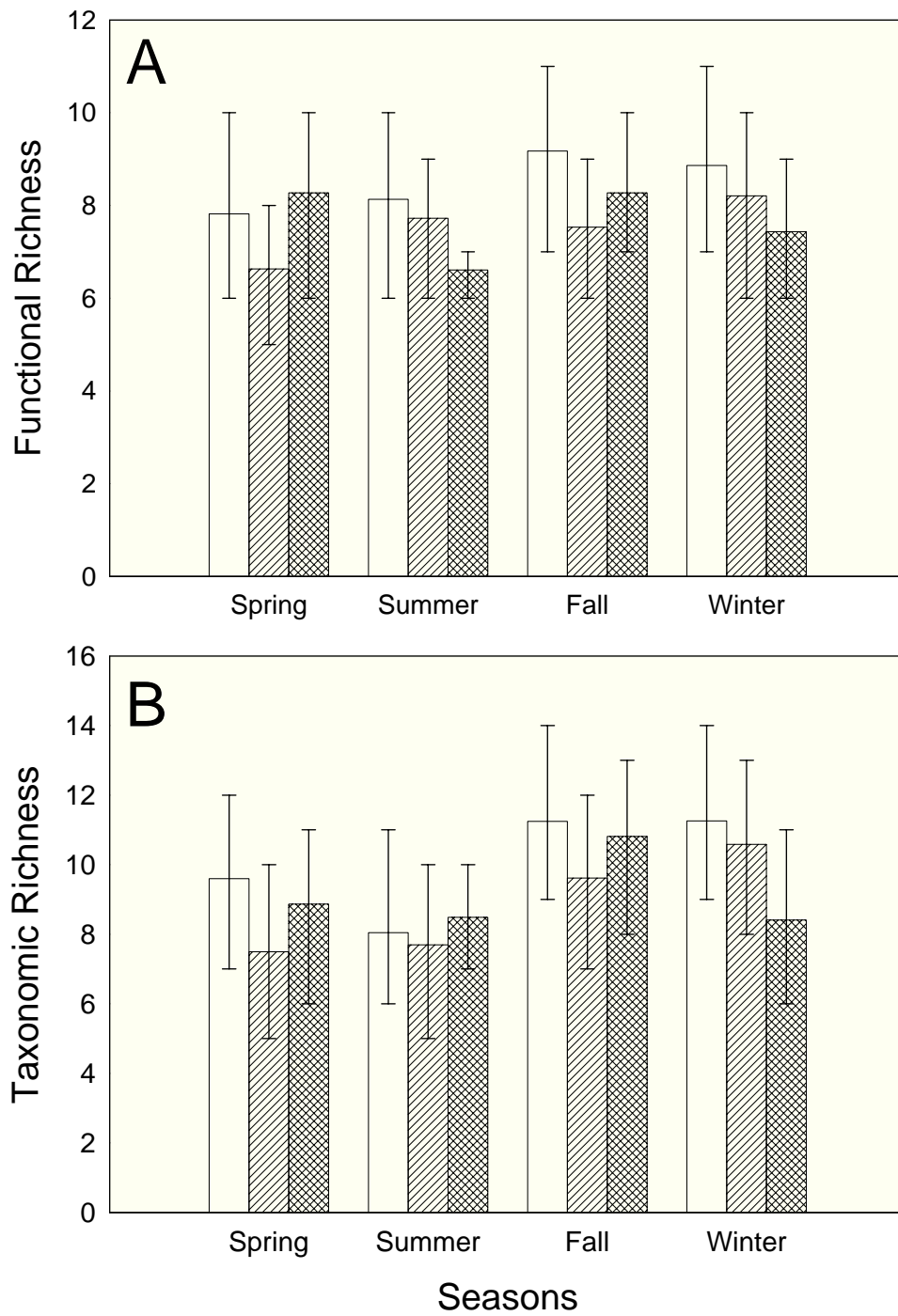


Figure 4.3. Rarefaction estimates of functional (A) and taxonomic (B) richness for three tributaries of the Colorado River across four seasons. Pedernales River has double hatch. San Saba River has single hatch. South Llano River has no hatch.

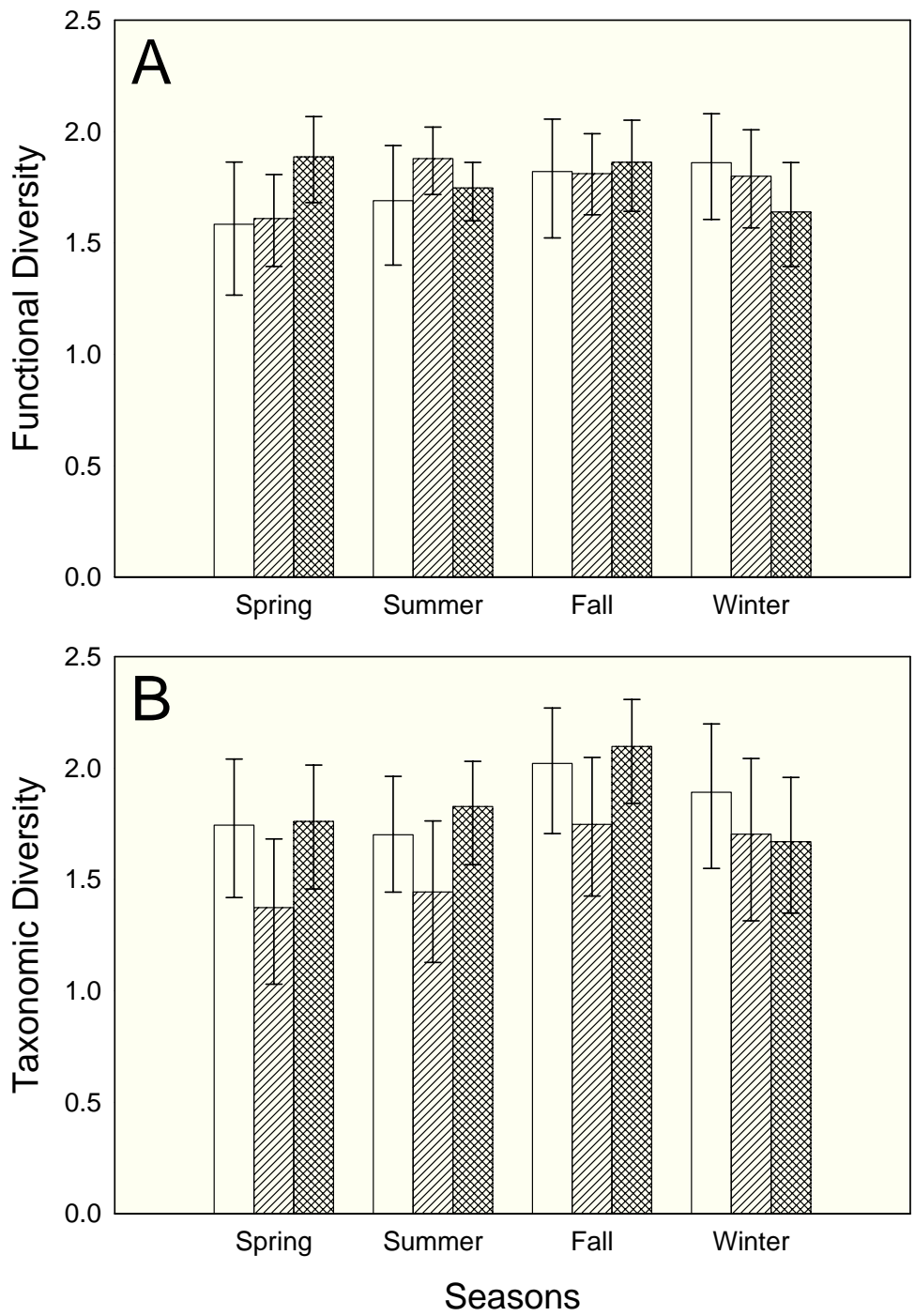


Figure 4.4. Rarefaction estimates of functional (A) and taxonomic (B) diversity for three tributaries of the Colorado River across four seasons. Pedernales River has double hatch. San Saba River has single hatch. South Llano River has no hatch.

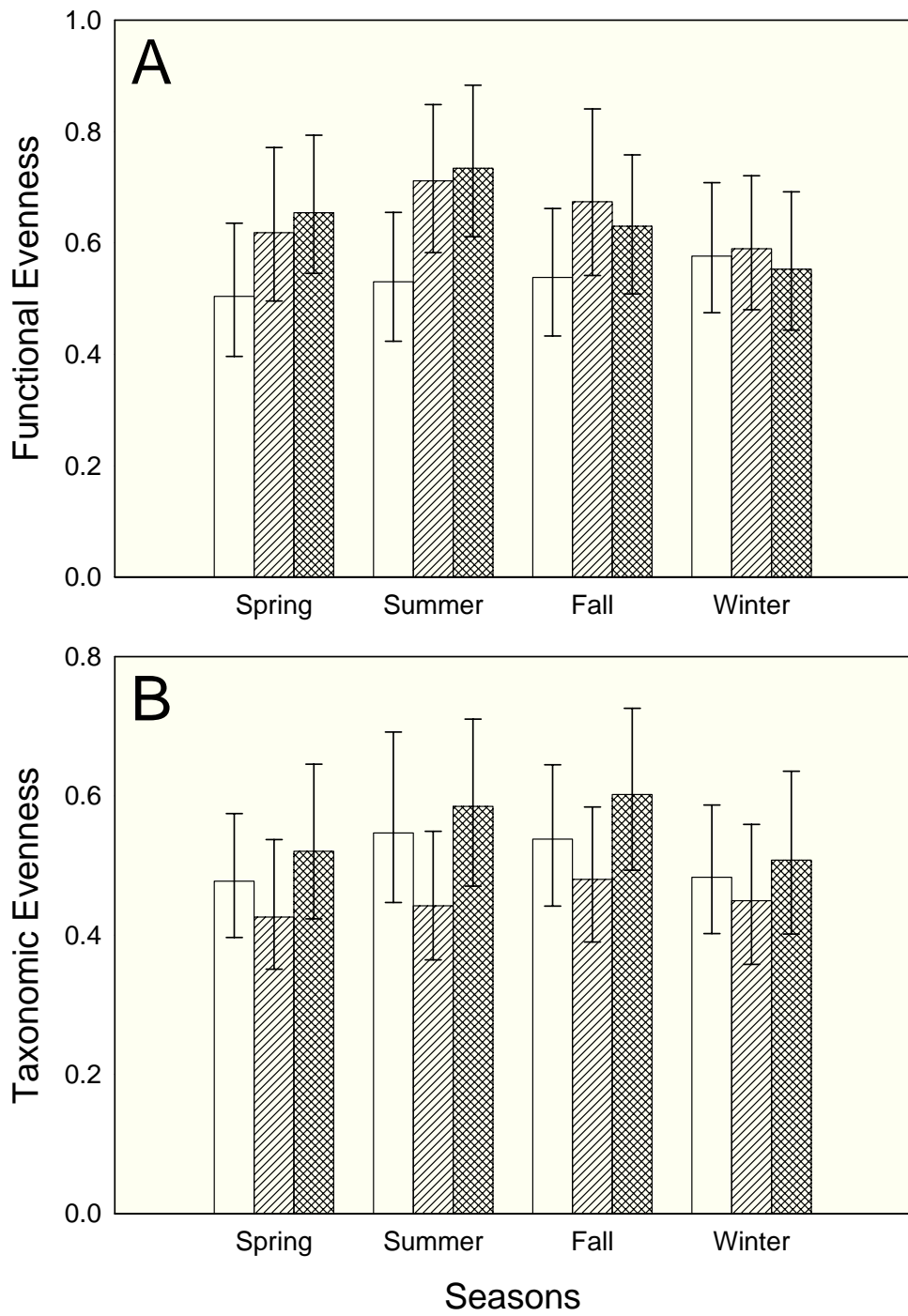


Figure 4.5. Rarefaction estimates of functional (A) and taxonomic (B) evenness for three tributaries of the Colorado River across four seasons. Pedernales River has double hatch. San Saba River has single hatch. South Llano River has no hatch.

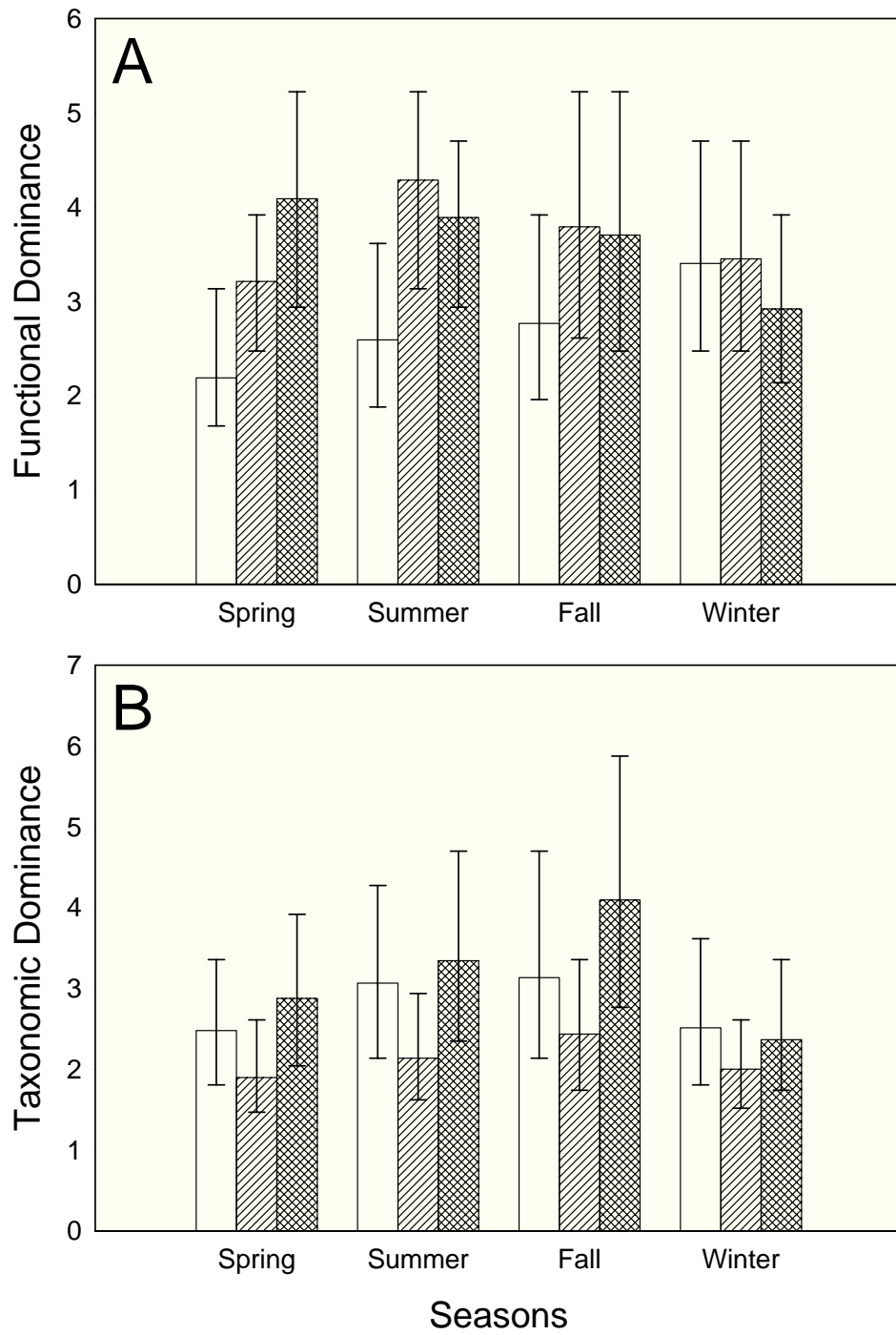


Figure 4.6. Rarefaction estimates of functional (A) and taxonomic (B) dominance for three tributaries of the Colorado River across four seasons. Pedernales River has double hatch. San Saba River has single hatch. South Llano River has no hatch.

CHAPTER V

DISCUSSION

In a seminal paper in stream ecology, Kenneth Cummins (1974) laid the foundation for future studies on the structure and function of stream ecosystems. He highlighted the importance of process-oriented questions in stream ecology, particularly as they related to ecosystem function. More importantly, he developed a classification scheme for functional feeding groups of macroinvertebrates that was partially independent of taxonomic identities. The major categories he suggested were shredders, grazers, collectors, and predators. Shredders tear and shred coarse particulate organic matter (CPOM) while feeding, which converts CPOM into fine particulate organic matter (FPOM) by physical means and in the form of fecal pellets. This allows other organisms to consume the FPOM. Grazers scrape algae and periphyton from rocks and other submerged objects. Like shredders, grazers also convert CPOM into FPOM in the form of fecal pellets and dislodgement of algal cells. Collectors almost exclusively feed on FPOM and can be further subdivided into filtering-collectors and gathering-collectors. Filtering-collectors gather food by filtering FPOM from the water column; whereas, gathering-collectors collect FPOM from wherever they can find available resources. Predators, as the name implies, feed on other animals adding another layer in the food web structure of stream ecosystems. Although the functional groupings of macroinvertebrates contributed greatly to the understanding of structure and function of stream ecosystems, it provides little insight into the role fishes play in stream ecosystems.

Several attempts have been made to categorize fishes into groups in order to facilitate understanding of complex ecological interactions among fishes. Most of this work has focused on the guild concept (Root 1967). In stream fishes, guilds are often used to simplify multiple-species assemblages and have been used to examine local assemblage structure (Schlosser 1982; Bain et al. 1988; Douglas and Matthews 1992; Grossman et al. 1998), biotic integrity (Gorman and Karr 1978; Schleiger 2000; Smogor and Angermeier 2001), diet selection (Horwitz 1978; Schlosser 1985), habitat use (Leonard and Orth 1988; Aadland 1993; Zorn et al. 2002), and reproductive strategies (Page and Swofford 1984). Despite the frequent use of guilds in stream-fish ecology, few studies have attempted to extend these groupings to examine the relationship between fishes and ecosystem level processes (but see Winemiller [1995] for a review of the relationships between biological diversity and ecological diversity in stream fishes). That is, little work has been done to develop functional groupings in stream fishes.

The classification scheme proposed by William Matthews (1998) was a positive step towards increasing the depth and breadth of our understanding of the role fishes play in ecosystem level processes. His classification scheme, however, does have weaknesses. First, the functional groupings have not been tested for empirical differences in ecosystem function. That is, we have no information on whether or not suction piscivores actually differ from biting piscivores in terms of nutrient cycling or decomposition rates. Second, assigning species to functional groups is inherently difficult. Many fishes are opportunistic and will vary their feeding behavior with environmental conditions. In addition, most fishes change their feeding behavior through

ontogeny. Thus, categorizing species into functional groups is unfortunately more subjective than objective. This was amplified by the fact that I was not intimately familiar with many of the species found throughout Texas; consequently, I relied on previous literature to classify species into functional groups. Despite these limitations, I believe the classification scheme proposed by Matthews provides a descent and initial framework with which to assess macroecological patterns in functional diversity of stream fishes. Macroecology focuses on broad spatial and temporal scales to increase ecological understanding. As a result, macroecologists generally do not incorporate fine-scale details, for they only mask course-scale patterns. This is not to say that behavioral ecologists are wrong for incorporating fine-scale data; rather, every ecologist must define their domain and work with within their constraints. I have chosen to examine macroecological patterns of functional diversity in stream fishes because of its relevance to contemporary ecology and because it is an area that needs much attention, especially given the loss of biodiversity that is occurring worldwide.

Biodiversity and ecosystem function is an important topic in contemporary ecology. It is driven by the fundamental need to understand how ecosystem level processes are affected by the cosmopolitan loss of biodiversity. Previous research has demonstrated decreases in taxonomic diversity, primarily species richness, clearly affect ecosystem function (Naeem et al. 1994; Tilman et al. 1996; McGrady-Steed et al. 1997; Wardle et al. 1997), ecosystem resilience (McNaughton 1977; Tilman et al. 1996; Naeem and Li 1997), and ecosystem variability (Frank and McNaughton 1991; Tilman and Downing 1994; Tilman 1996). However, a mechanistic understanding remains elusive,

especially as it relates to community structure (Hooper et al. 2005). The studies included in this dissertation help shed light into the relationship between ecosystem function and community structure, at least for temperate stream ecosystems with moderate levels of taxonomic diversity.

Strong correlations exist between functional and taxonomic diversity, with each aspect of functional diversity (i.e., richness, diversity, evenness, and dominance) being most highly correlated with the corresponding aspect of taxonomic diversity. However, the relationships are nonlinear, indicating stream fish are functionally redundant. Functional redundancy is a characteristic of species within an ecosystem where certain species contribute in equivalent ways to an ecosystem function such that one species may substitute for another, although the concept of functional redundancy may be inconsistent with stable coexistence (Loreau 2004). Nevertheless, functional redundancy is important for ecosystem resistance to environmental perturbations (Naeem and Li 1997). Thus, maintaining functionally equivalent species in managed ecosystems should be a primary concern for conservation and management agencies alike.

Stream fish are typically plastic in their feeding behavior, resulting from ontogenetic changes in feeding modes and opportunistic strategies (Gerking 1994). This plasticity is also true for mechanisms that structure stream-fish assemblages, from both functional and taxonomic perspectives. However, fish assemblages are generally more evenly distributed in terms of functional groups than species. Consequently, the potential underlying mechanisms that structure them are those that result in fairly even distributions (e.g., broken-stick and dominance decay models) as opposed to those

resulting in highly dominated systems (e.g., dominance preemption). This pattern is most easily observed when examining individual localities than pooled assemblages, although assemblages pooled according to river basin more closely resemble the individual localities than assemblages pooled according to ecoregions. This suggests scale dependence in structuring mechanisms of stream-fish assemblages. Thus, future studies examining the underlying mechanisms that structure stream-fish assemblages should clearly delineate the spatial scale

In terms of predictability, broad-scale, biogeographic variables predicted twice as much of the variation in taxonomic diversity as functional diversity, although neither would be considered highly predictable with only 22% of the variation in taxonomic diversity and 10% of the variation in functional diversity accounted for by the broad-scale, abiotic variables. This finding contrasts similar studies that found functional organization of fish assemblages to be associated with hydrological variability (Poff and Allan 1995; Goldstein and Meador 2004). Fine-scale, abiotic variables, on the other hand, were found to be good predictors of functional and taxonomic diversity at the local level. This suggests that functional and taxonomic diversity are more of a result of local abiotic conditions than broad scale factors.

Despite seasonal variation in energy availability within a stream, fish assemblages within rivers were more similar to assemblages from the same river than assemblages from different rivers, regardless of season, from both taxonomic and functional perspectives. This is in contrast to a priori predictions that assemblages from different rivers would be more closely related to one another within a season from a functional

perspective, but assemblages within a river will be more similar to one another regardless of season from a taxonomic perspective. This indicates that the relative abundance of functional groups does not change temporally, at least with respect to changes in taxonomic diversity. Hence, traditional structuring mechanisms that have been identified with respect to species coexistence may still hold in regards to functional diversity as well.

The results of these studies provide a different perspective of looking at the relationship between biodiversity and ecosystem function by incorporating aspects of both functional and taxonomic diversity. Studies of biodiversity have taken center stage in ecology over the past 20 years. However, much of the current work on biodiversity focuses on taxonomic diversity rather than functional diversity. Although correlations exist between the two aspects of biodiversity, they characterize different aspects of assemblage structure and provide complementary insight into the overall relationship between biodiversity and ecosystem function. In fact, the “functioning of an ecosystem is not governed by the phylogenetic content of its biota, but by the functional traits of individuals, the distribution and abundance of these individuals, and their biological activity” (Naeem and Wright 2003). Consequently, it is imperative that future studies addressing issues regarding biodiversity and ecosystem function make explicit use of functional groups or at least incorporate the functional attributes of individuals.

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APPENDIX A

FUNCTIONAL GROUPINGS OF STREAM FISH

Table A.1. Functional groupings of stream fish: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

Scientific Name	A	B	C	D	E	F	G	H	I	J	K	L	M	N
<i>Lepisosteus oculatus</i>	0	0	0	0	0	0	0	0	X	0	0	0	0	X
<i>Lepisosteus osseus</i>	0	0	0	0	0	0	0	0	X	0	0	0	0	X
<i>Lepisosteus spatula</i>	0	0	0	0	0	0	0	0	X	0	0	0	0	X
<i>Anguilla rostrata</i>	0	0	0	0	0	0	0	0	0	X	0	X	0	X
<i>Dorosoma cepedianum</i>	0	0	X	0	0	0	0	X	0	0	0	0	0	0
<i>Dorosoma petenense</i>	0	0	0	0	0	0	0	X	0	X	0	0	0	0
<i>Esox americanus</i>	0	0	0	0	0	0	0	0	0	X	0	0	X	0
<i>Astyanax mexicanus</i>	0	X	0	0	0	0	0	0	0	X	0	0	0	X
<i>Campostoma anomalum</i>	X	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Campostoma ornatum</i>	X	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cyprinella lutrensis</i>	0	X	0	0	0	0	0	0	0	X	0	0	0	0
<i>Cyprinella proserpina</i>	0	0	0	0	0	0	0	0	X	X	X	0	0	0
<i>Cyprinella venusta</i>	0	0	X	0	0	0	0	0	0	X	X	0	0	0
<i>Cyprinus carpio</i>	0	X	0	X	0	X	X	0	0	0	0	X	0	0
<i>Dionda episcopa</i>	0	X	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hybognathus hayi</i>	X	0	0	X	0	0	0	0	0	0	0	0	0	0
<i>Hybognathus nuchalis</i>	X	0	0	X	0	0	0	0	0	0	0	0	0	0
<i>Hybognathus placitus</i>	X	0	0	X	0	0	0	0	0	0	0	0	0	0
<i>Luxilus chrysocephalus</i>	0	X	0	0	0	0	0	0	0	X	X	0	0	0
<i>Lythrurus fumeus</i>	0	0	X	0	0	0	0	0	X	X	X	0	0	0
<i>Lythrurus umbratilis</i>	0	0	0	0	0	0	0	0	X	X	X	0	0	0
<i>Macrhybopsis aestivalis</i>	0	0	0	0	0	0	0	0	X	X	X	0	0	0
<i>Notemigonus crysoleucas</i>	0	0	0	0	0	0	X	X	0	X	0	0	0	0
<i>Notropis amabilis</i>	0	0	0	0	0	0	0	0	X	X	X	0	0	0
<i>Notropis atrocaudalis</i>	0	0	0	0	0	0	0	0	X	X	X	0	0	0
<i>Notropis bairdi</i>	0	0	0	0	0	0	0	0	X	X	X	0	0	0
<i>Notropis braytoni</i>	0	0	0	0	0	0	0	0	X	X	X	0	0	0

<i>Notropis chalybeus</i>	X	0	0	0	0	0	0	0	0	X	X	0	0	0
<i>Notropis chihuahua</i>	0	0	0	0	0	0	0	0	X	X	X	0	0	0
<i>Notropis sabiniae</i>	0	0	0	0	0	0	0	0	X	X	X	0	0	0
<i>Notropis stramineus</i>	0	X	0	0	0	0	0	0	0	X	X	0	0	0
<i>Notropis texanus</i>	0	0	X	0	0	0	0	0	X	X	X	0	0	0
<i>Notropis volucellus</i>	0	0	X	0	0	0	0	0	X	X	X	0	0	0
<i>Opsopoeodus emiliae</i>	X	0	0	0	0	0	X	0	X	X	0	0	0	0
<i>Phenacobis mirabilis</i>	0	0	X	0	0	0	0	0	0	0	X	0	0	0
<i>Pimephales promelas</i>	0	X	0	X	0	0	X	0	0	0	0	0	0	0
<i>Pimephales vigilax</i>	0	0	X	0	0	0	0	0	0	0	X	0	0	0
<i>Carpiodes carpio</i>	X	0	X	0	0	0	0	0	0	0	X	0	0	0
<i>Erimyzon oblongus</i>	X	0	X	0	0	0	0	0	0	0	X	0	0	0
<i>Erimyzon sucetta</i>	X	0	X	0	0	0	0	0	0	0	X	0	0	0
<i>Ictiobus bubalus</i>	X	0	X	0	0	0	0	0	0	0	X	X	0	0
<i>Minytrema melanops</i>	X	0	X	0	0	0	0	0	0	0	X	0	0	0
<i>Moxostoma congestum</i>	0	0	0	0	0	0	0	0	0	0	X	X	0	0
<i>Moxostoma poecilurum</i>	0	0	X	0	0	0	0	0	0	0	X	0	0	0
<i>Ameiurus melas</i>	0	0	0	0	0	X	0	0	0	0	0	X	X	0
<i>Ameiurus natalis</i>	0	0	0	0	0	X	0	0	0	0	0	X	X	0
<i>Ictalurus furcatus</i>	0	0	0	0	0	X	0	0	0	0	X	X	X	0
<i>Ictalurus lupus</i>	0	0	0	0	0	X	0	0	0	0	X	0	X	0
<i>Ictalurus punctatus</i>	0	0	0	0	0	X	0	0	0	0	0	0	X	0
<i>Noturus gyrinus</i>	0	0	0	0	0	0	0	0	0	0	X	0	0	0
<i>Noturus nocturnus</i>	0	0	0	0	0	0	0	0	0	0	X	0	0	X
<i>Pylodictis olivaris</i>	0	0	0	0	0	0	0	0	0	0	X	X	X	0
<i>Aphredoderus sayanus</i>	0	0	0	0	0	0	0	0	0	X	0	0	X	0
<i>Cyprinodon eximius</i>	0	0	0	0	0	0	0	0	X	0	0	0	0	0
<i>Cyprinodon rubrofluviatilis</i>	0	0	0	0	0	0	0	0	X	0	0	0	0	0
<i>Fundulus notatus</i>	0	0	0	0	0	0	0	0	X	0	X	0	0	0
<i>Fundulus olivaceus</i>	0	0	0	0	0	0	0	0	X	0	0	0	0	0
<i>Fundulus zebrinus</i>	0	0	0	0	X	0	0	0	X	0	0	0	0	0
<i>Gambusia affinis</i>	0	0	0	0	0	0	X	0	X	0	0	0	0	0
<i>Gambusia geiseri</i>	0	0	0	0	0	0	0	0	X	0	0	0	0	0
<i>Poecilia latipinna</i>	0	X	0	0	0	0	0	0	0	X	0	0	0	0
<i>Labidesthes sicculus</i>	0	0	0	0	0	0	0	X	0	X	0	0	0	0
<i>Centrarchus macropterus</i>	0	0	0	0	0	0	0	0	0	X	0	0	0	0

<i>Elassoma zonatum</i>	0	0	0	0	0	0	0	0	X	X	X	0	0	0
<i>Lepomis auritus</i>	0	0	0	0	0	0	0	0	X	X	0	X	X	0
<i>Lepomis cyanellus</i>	0	0	0	0	0	0	0	0	X	X	0	0	X	0
<i>Lepomis gulosus</i>	0	0	0	0	0	0	0	0	X	X	0	0	X	0
<i>Lepomis humilis</i>	0	0	0	0	0	0	0	0	X	X	0	0	0	0
<i>Lepomis macrochirus</i>	0	0	0	0	0	0	X	0	X	X	0	0	X	0
<i>Lepomis marginatus</i>	0	0	0	0	0	0	0	0	X	X	0	0	0	0
<i>Lepomis megalotis</i>	0	0	0	0	0	0	X	0	X	X	0	0	X	0
<i>Lepomis microlophus</i>	0	0	0	0	0	0	0	0	X	X	0	X	0	0
<i>Lepomis punctatus</i>	0	0	0	0	0	0	0	0	X	X	0	X	0	0
<i>Lepomis symmetricus</i>	0	0	0	0	0	0	0	0	X	X	0	X	0	0
<i>Micropterus dolomieu</i>	0	0	0	0	0	0	0	0	0	X	0	0	X	0
<i>Micropterus punctatus</i>	0	0	0	0	0	0	0	0	0	X	0	0	X	0
<i>Micropterus salmoides</i>	0	0	0	0	0	0	X	0	0	X	0	X	X	0
<i>Micropterus treculi</i>	0	0	0	0	0	0	0	0	0	X	0	0	X	0
<i>Pomoxis annularis</i>	0	0	0	0	0	0	0	X	0	X	0	0	X	0
<i>Pomoxis nigromaculatus</i>	0	0	0	0	0	0	0	0	0	X	0	0	X	0
<i>Ammocrypta vivax</i>	0	0	0	0	0	0	0	0	0	0	X	0	0	0
<i>Etheostoma asprigene</i>	0	0	0	0	0	0	0	0	0	0	X	0	0	0
<i>Etheostoma chlorosomum</i>	0	0	0	0	0	0	0	0	0	0	X	0	0	0
<i>Etheostoma gracile</i>	0	0	0	0	0	0	0	0	0	0	X	0	0	0
<i>Etheostoma grahami</i>	0	0	0	0	0	0	0	0	0	0	X	0	0	0
<i>Etheostoma lepidum</i>	X	X	0	0	0	0	0	0	0	0	X	0	0	0
<i>Etheostoma parvipinne</i>	0	0	0	0	0	0	0	0	0	0	X	0	0	0
<i>Etheostoma proeliare</i>	0	0	0	0	0	0	0	0	0	0	X	0	0	0
<i>Etheostoma radiosum</i>	0	0	0	0	0	0	0	0	0	0	X	0	0	0
<i>Etheostoma spectabile</i>	0	0	0	0	0	0	X	0	0	0	X	0	0	0
<i>Etheostoma whipplei</i>	0	0	0	0	0	0	0	0	0	0	X	0	0	0
<i>Percina carbonaria</i>	0	0	0	0	X	0	0	0	0	0	X	0	0	0
<i>Percina macrolepida</i>	0	0	0	0	X	0	0	0	0	0	X	0	0	0
<i>Percina sciera</i>	0	0	0	0	X	0	0	0	0	0	X	0	0	0
<i>Aplodinotus grunniens</i>	0	0	0	0	0	0	0	0	0	0	X	X	0	X
<i>Cichlasoma cyanoguttatum</i>	0	0	X	0	0	0	0	0	0	X	X	X	0	0
<i>Tilapia aurea</i>	0	X	0	0	0	0	0	X	0	0	0	0	0	0

Table A.2. References used to classify fish species into functional groups.

Scientific Name	Common name	References
<i>Lepisosteus oculatus</i>	Spotted gar	A B C D E F
<i>Lepisosteus osseus</i>	Longnose gar	A B C D E F
<i>Lepisosteus spatula</i>	Alligator gar	B F
<i>Anguilla rostrata</i>	American eel	A B C D E F
<i>Dorosoma cepedianum</i>	Gizzard shad	A B C D E F
<i>Dorosoma petenense</i>	Threadfin shad	A B C E F
<i>Esox americanus</i>	Grass pickerel	A B C D F
<i>Astyanax mexicanus</i>	Mexican tetra	B E F
<i>Campostoma anomalum</i>	Central stoneroller	A B C D E F
<i>Campostoma ornatum</i>	Mexican stoneroller	B
<i>Cyprinella lutrensis</i>	Red shiner	A B C E F
<i>Cyprinella proserpina</i>	Proserpine shiner	B
<i>Cyprinella venusta</i>	Blacktail shiner	A B C
<i>Cyprinus carpio</i>	Common carp	A B C D E F
<i>Dionda episcopa</i>	Roundnose minnow	B E
<i>Hybognathus hayi</i>	Cypress minnow	A B C
<i>Hybognathus nuchalis</i>	Mississippi silvery minnow	A B C D
<i>Hybognathus placitus</i>	Plains minnow	A B D E F
<i>Luxilus chrysocephalus</i>	Striped minnow	A B C
<i>Lythrurus fumeus</i>	Ribbon shiner	A B C
<i>Lythrurus umbratilis</i>	Redfin shiner	A B C D F
<i>Macrhybopsis aestivalis</i>	Speckled chub	B C
<i>Notemigonus crysoleucas</i>	Golden shiner	A B C D E F
<i>Notropis amabilis</i>	Texas shiner	B E
<i>Notropis atrocaudalis</i>	Blackspot shiner	A B
<i>Notropis bairdi</i>	Red River shiner	A B
<i>Notropis braytoni</i>	Tamaulipas shiner	B
<i>Notropis chalybeus</i>	Ironcolor shiner	A B C
<i>Notropis chihuahua</i>	Chihuahua shiner	B
<i>Notropis sabinae</i>	Sabine shiner	B C
<i>Notropis stramineus</i>	Sand shiner	A B D E F
<i>Notropis texanus</i>	Weed shiner	B C
<i>Notropis volucellus</i>	Mimic shiner	A B C D
<i>Opsopoeodus emiliae</i>	Pugnose minnow	A B C D
<i>Phenacobis mirabilis</i>	Suckermouth minnow	A B C E
<i>Pimephales promelas</i>	Fathead minnow	A B C D E

<i>Pimephales vigilax</i>	Bullhead minnow	A	B	C	E	
<i>Carpionodes carpio</i>	River carpsucker	A	B	C	E	F
<i>Erimyzon oblongus</i>	Creek chubsucker	A	B	C	D	F
<i>Erimyzon sucetta</i>	Lake chubsucker	A	B	C	D	F
<i>Ictiobus bubalus</i>	Smallmouth buffalo	A	B	C	D	E F
<i>Minytrema melanops</i>	Spotted sucker	A	B	C	D	F
<i>Moxostoma congestum</i>	Gray redhorse	B	E	F		
<i>Moxostoma poecilurum</i>	Blacktail redhorse	B	C			
<i>Ameiurus melas</i>	Black bullhead	A	B	C	D	E F
<i>Ameiurus natalis</i>	Yellow bullhead	A	B	C	D	E F
<i>Ictalurus furcatus</i>	Blue catfish	A	B	C	E	F
<i>Ictalurus lupus</i>	Headwater catfish	B	E			
<i>Ictalurus punctatus</i>	Channel catfish	A	B	C	D	E F
<i>Noturus gyrinus</i>	Tadpole madtom	A	B	C	D	
<i>Noturus nocturnus</i>	Freckled madtom	A	B	C		
<i>Pylodictis olivaris</i>	Flathead catfish	A	B	C	D	E F
<i>Aphredoderus sayanus</i>	Pirate perch	A	B	C	F	
<i>Cyprinodon eximius</i>	Conchos pupfish	B				
<i>Cyprinodon rubrofluviatilis</i>	Red River pupfish	A	B	F		
<i>Fundulus notatus</i>	Blackstripe topminnow	A	B	C	F	
<i>Fundulus olivaceus</i>	Blackspotted topminnow	A	B	C		
<i>Fundulus zebrinus</i>	Plains killifish	A	B	E	F	
<i>Gambusia affinis</i>	Western mosquitofish	A	B	C	E	F
<i>Gambusia geiseri</i>	Largespring gambusia	B				
<i>Poecilia latipinna</i>	Sailfin molly	B	C	E		
<i>Labidesthes sicculus</i>	Brook silverside	A	B	C	D	F
<i>Centrarchus macropterus</i>	Flier	A	B	C	F	
<i>Elassoma zonatum</i>	Banded pygmy sunfish	A	B	C		
<i>Lepomis auritus</i>	Redbreast sunfish	A	B	C	D	F
<i>Lepomis cyanellus</i>	Green sunfish	A	B	C	D	E F
<i>Lepomis gulosus</i>	Warmouth	A	B	C	D	E F
<i>Lepomis humilis</i>	Orangespotted sunfish	A	B	C	F	
<i>Lepomis macrochirus</i>	Bluegill	A	B	C	D	E F
<i>Lepomis marginatus</i>	Dollar sunfish	A	B	C		
<i>Lepomis megalotis</i>	Longear sunfish	A	B	C	D	E F
<i>Lepomis microlophus</i>	Redear sunfish	A	B	C	E	F
<i>Lepomis punctatus</i>	Spotted sunfish	B	F			
<i>Lepomis symmetricus</i>	Bantam sunfish	A	B	C	F	

<i>Micropterus dolomieu</i>	Smallmouth bass	A	B	C	D	E	F
<i>Micropterus punctatus</i>	Spotted bass	A	B	C	D	E	F
<i>Micropterus salmoides</i>	Largemouth bass	A	B	C	D	E	F
<i>Micropterus treculi</i>	Guadalupe bass	B	F				
<i>Pomoxis annularis</i>	White crappie	A	B	C	D	E	F
<i>Pomoxis nigromaculatus</i>	Black crappie	A	B	C	D	E	F
<i>Ammocrypta vivax</i>	Scaly sand darter	A	B	C			
<i>Etheostoma asprigene</i>	Mud darter	A	B	C			
<i>Etheostoma chlorosomum</i>	Bluntnose darter	A	B	C			
<i>Etheostoma gracile</i>	Slough darter	A	B	C			
<i>Etheostoma grahami</i>	Rio Grande darter	B					
<i>Etheostoma lepidum</i>	Greenthroat darter	B					
<i>Etheostoma parvipinne</i>	Goldstripe darter	A	B	C			
<i>Etheostoma proeliare</i>	Cypress darter	A	B	C			
<i>Etheostoma radiosum</i>	Orangebelly darter	A	B				
<i>Etheostoma spectabile</i>	Orangethroat darter	A	B				
<i>Etheostoma whipplei</i>	Redfin darter	A	B	C			
<i>Percina carbonaria</i>	Texas logperch	B					
<i>Percina macrolepada</i>	Bigscale logperch	A	B	E			
<i>Percina sciera</i>	Dusky logperch	A	B	C			
<i>Aplodinotus grunniens</i>	Freshwater drum	A	B	C	E	F	
<i>Cichlasoma cyanoguttatum</i>	Rio Grande cichlid	B	F				
<i>Tilapia aurea</i>	Blue tilapia	B	C				

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APPENDIX B

RELATIVE ABUNDANCE OF FUNCTIONAL GROUPS FOR
STREAM-FISH ASSEMBLAGES ACROSS TEXAS

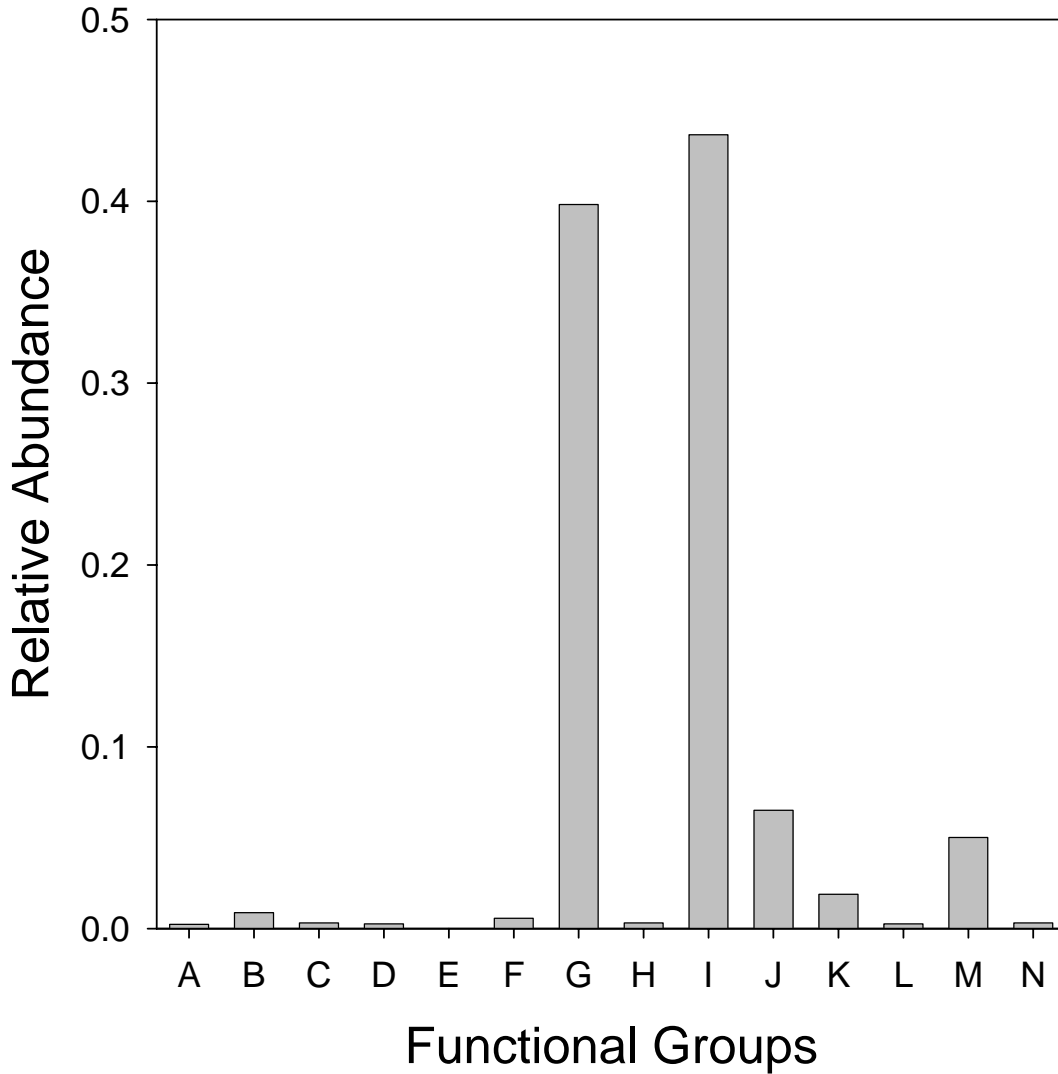


Figure B.1. Functional groupings of stream fish from West Bernard Creek, Wharton County, in the Brazos-Colorado River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

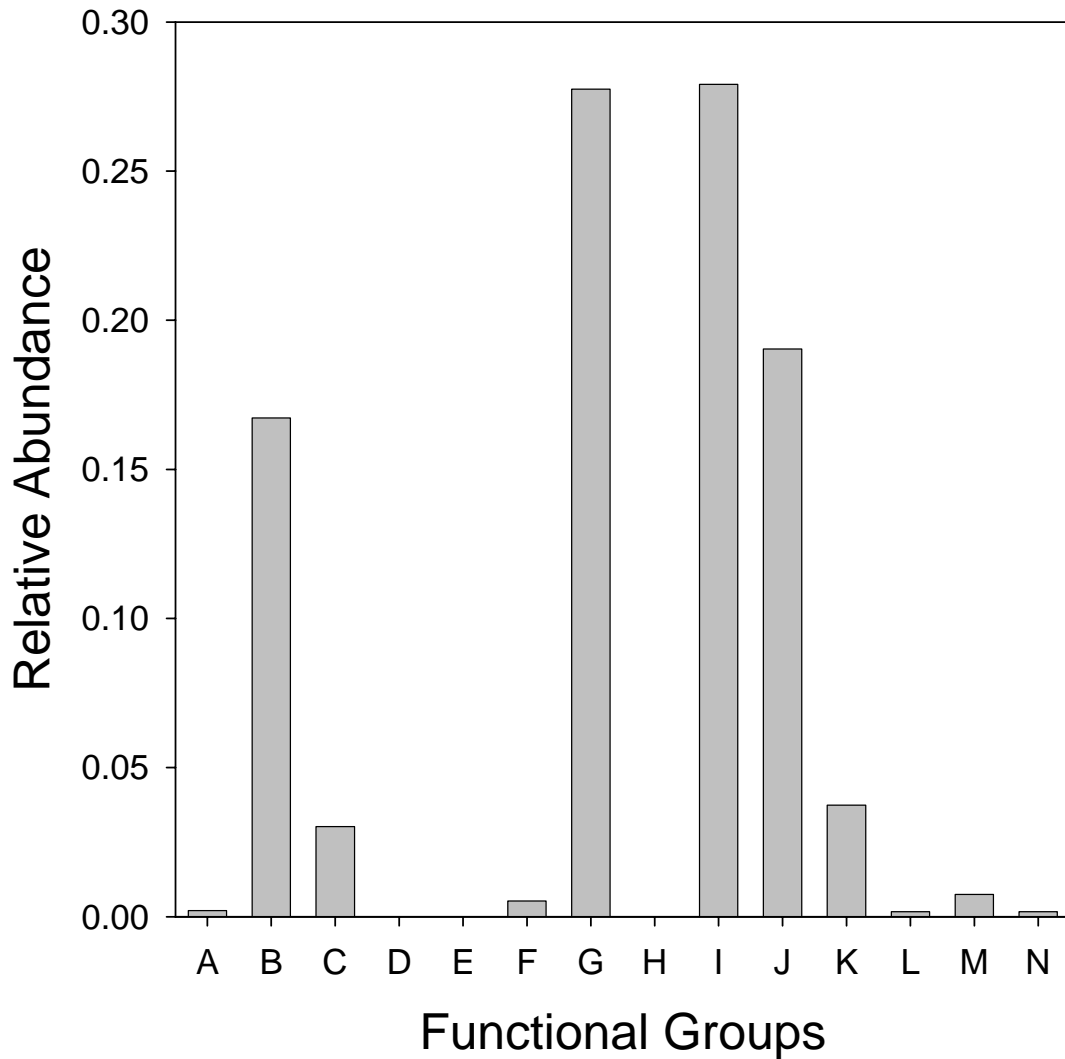


Figure B.2. Functional groupings of stream fish from West Mustang Creek, Wharton County, in the Lavaca River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

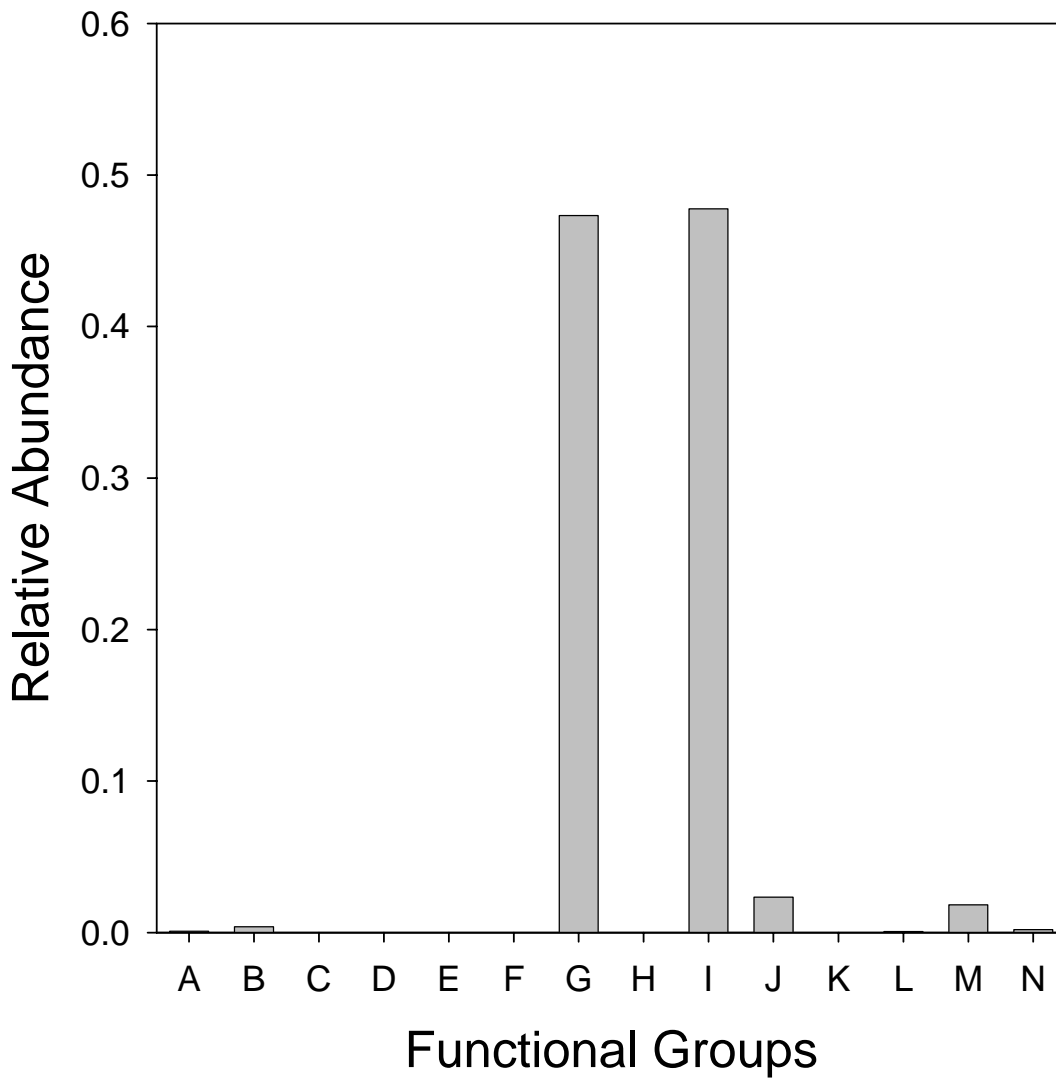


Figure B.3. Functional groupings of stream fish from Arenosa Creek, Jackson County, in the Lavaca-Guadalupe River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

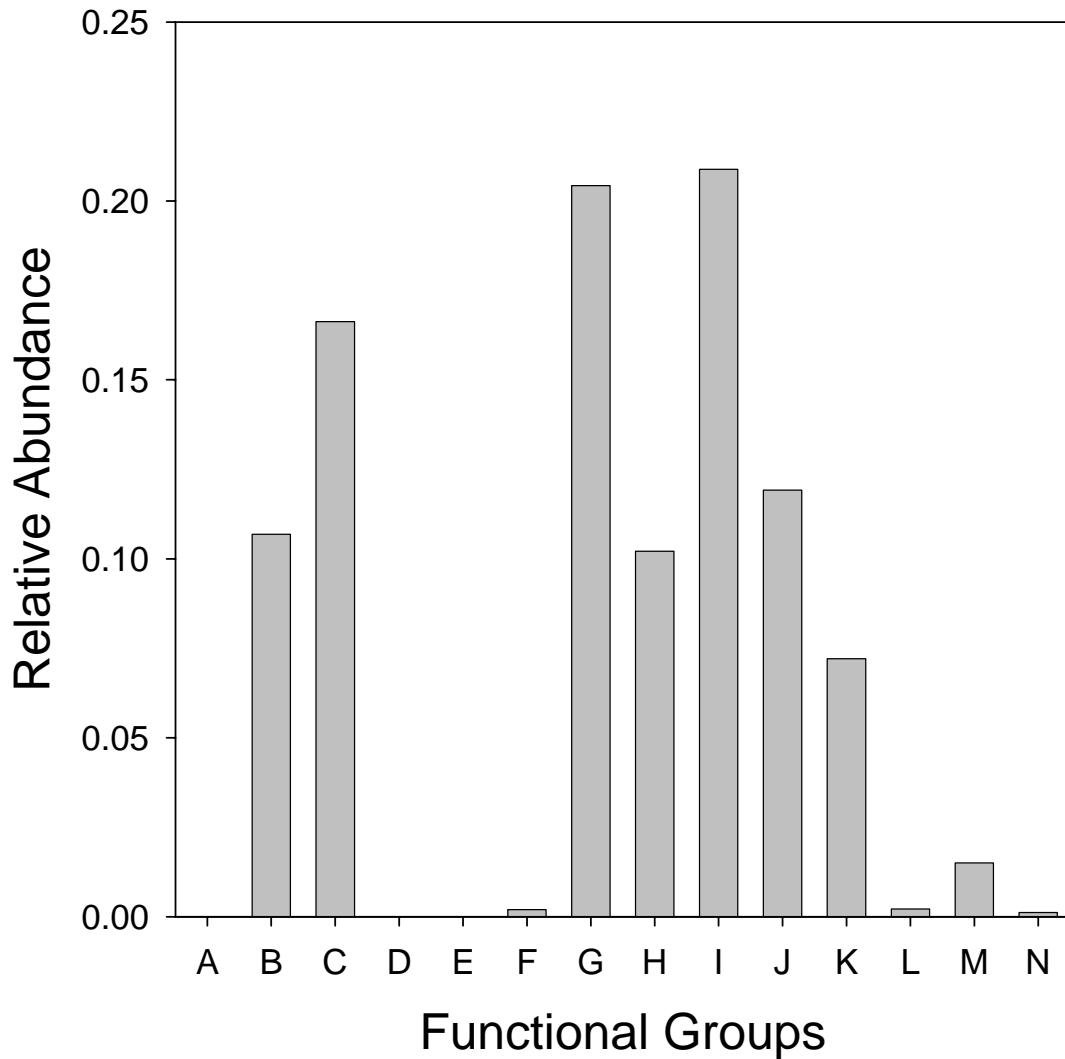


Figure B.4. Functional groupings of stream fish from Big Creek, Fort Bend County, in the Brazos River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

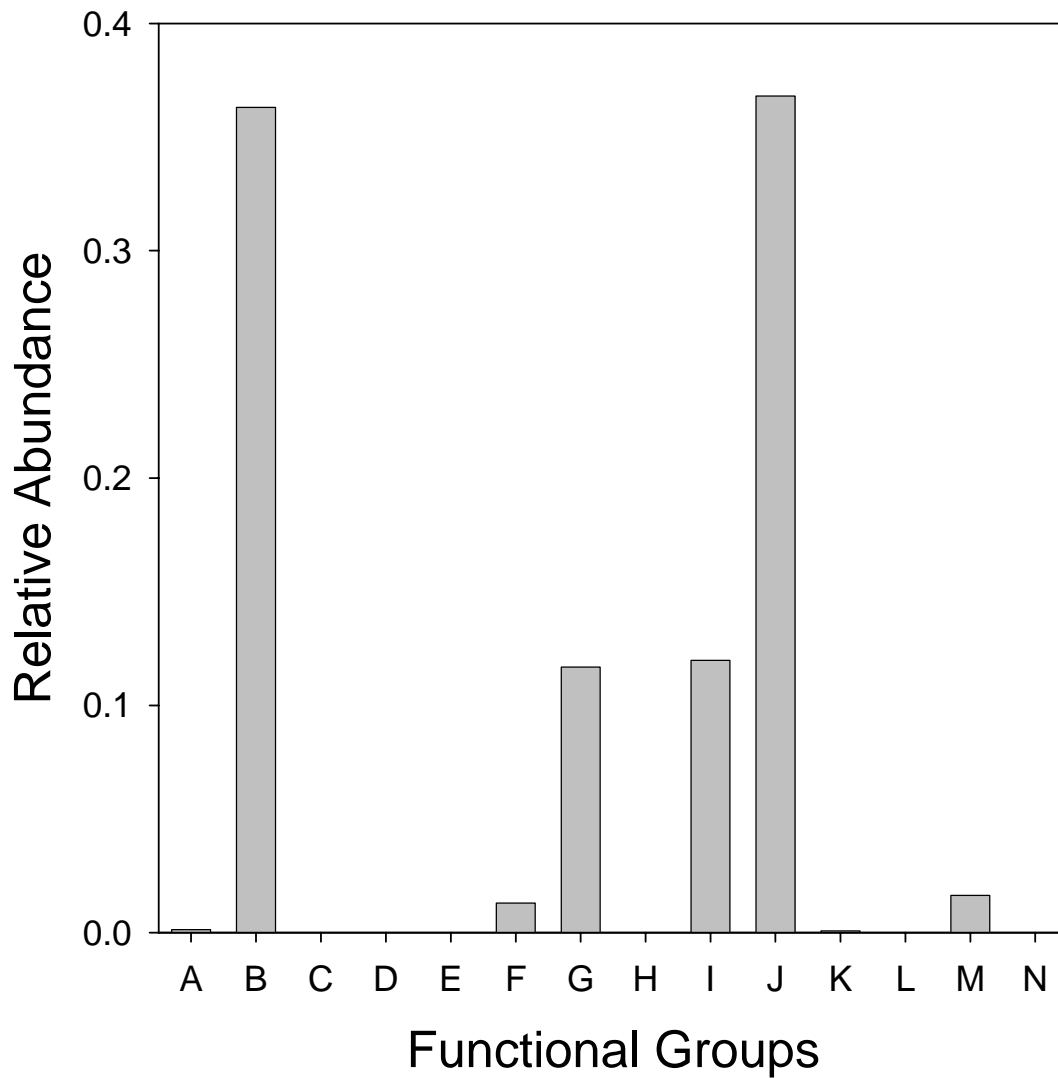


Figure B.5. Functional groupings of stream fish from West Carancahua Creek, Jackson County, in the Colorado-Lavaca River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

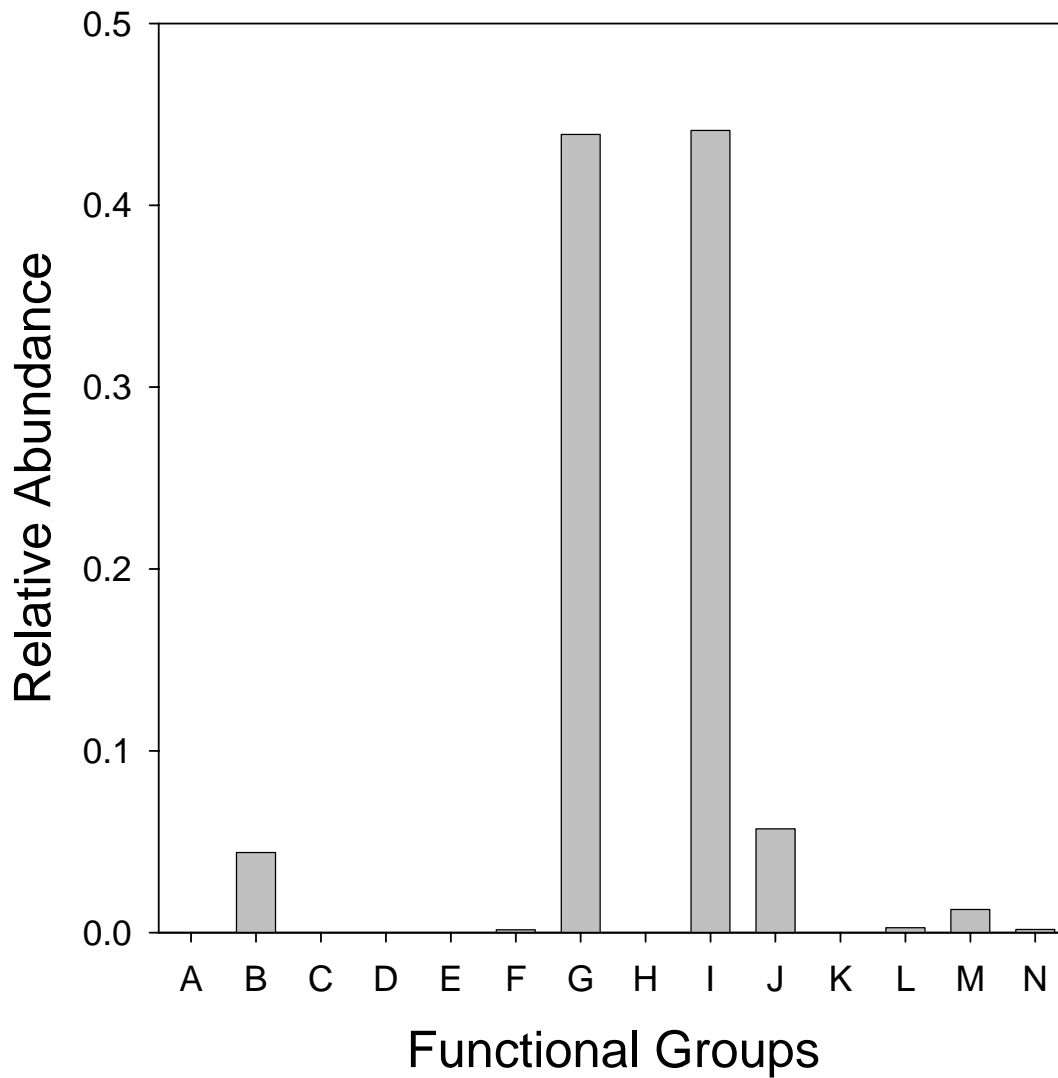


Figure B.6. Functional groupings of stream fish from Placedo Creek, Victoria County, in the Lavaca-Guadalupe River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

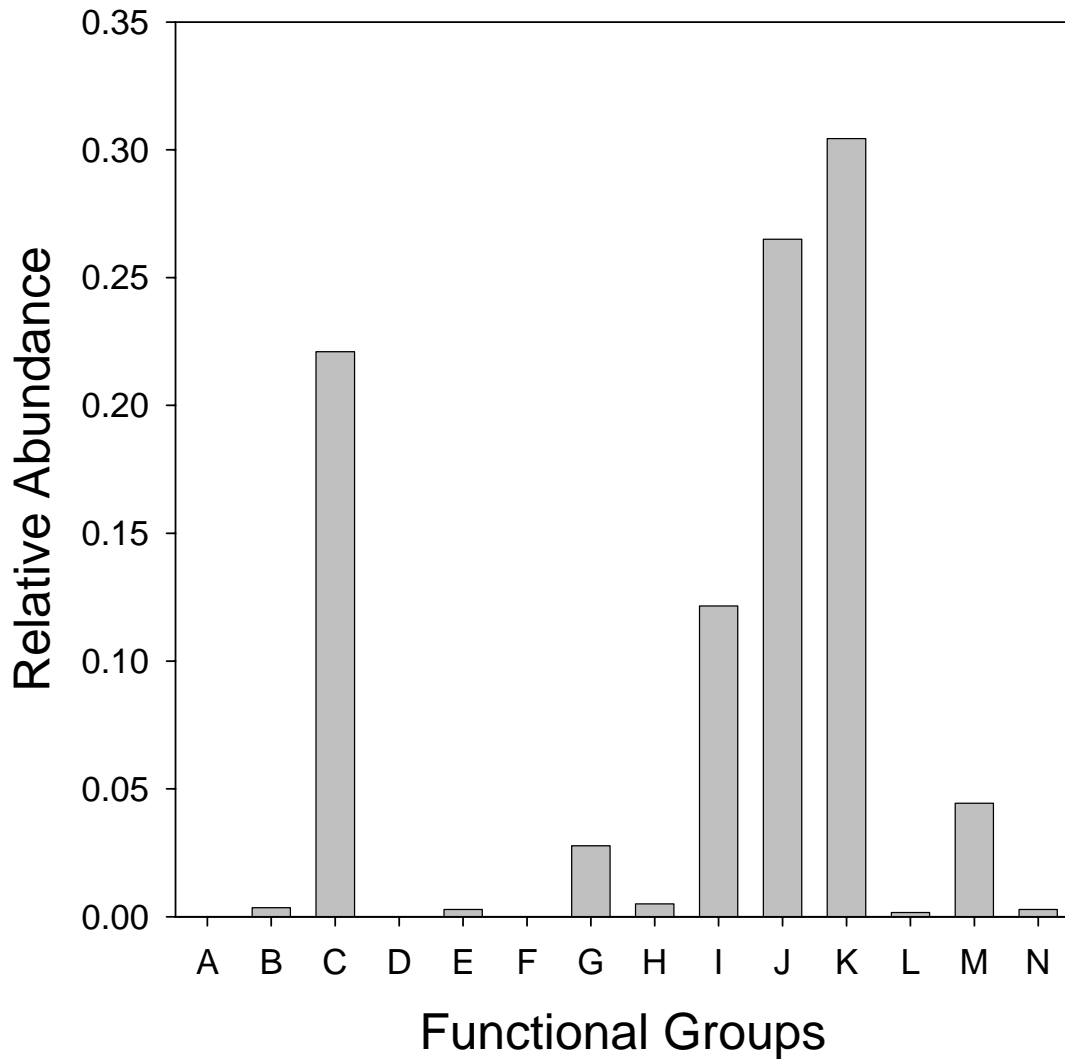


Figure B.7. Functional groupings of stream fish from Lake Creek, Montgomery County, in the San Jacinto River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

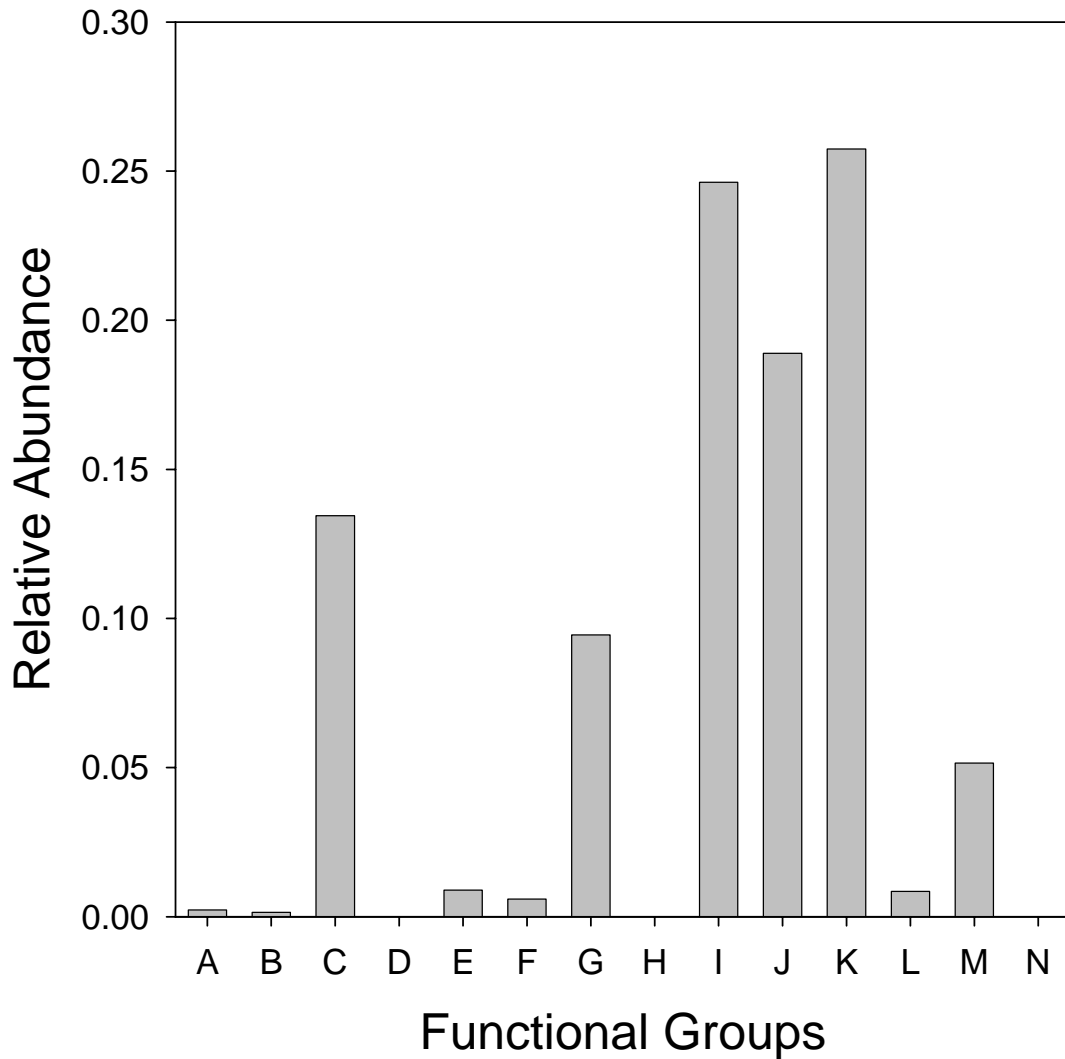


Figure B.8. Functional groupings of stream fish from Little Cypress Creek, Upshur County, in the Cypress River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

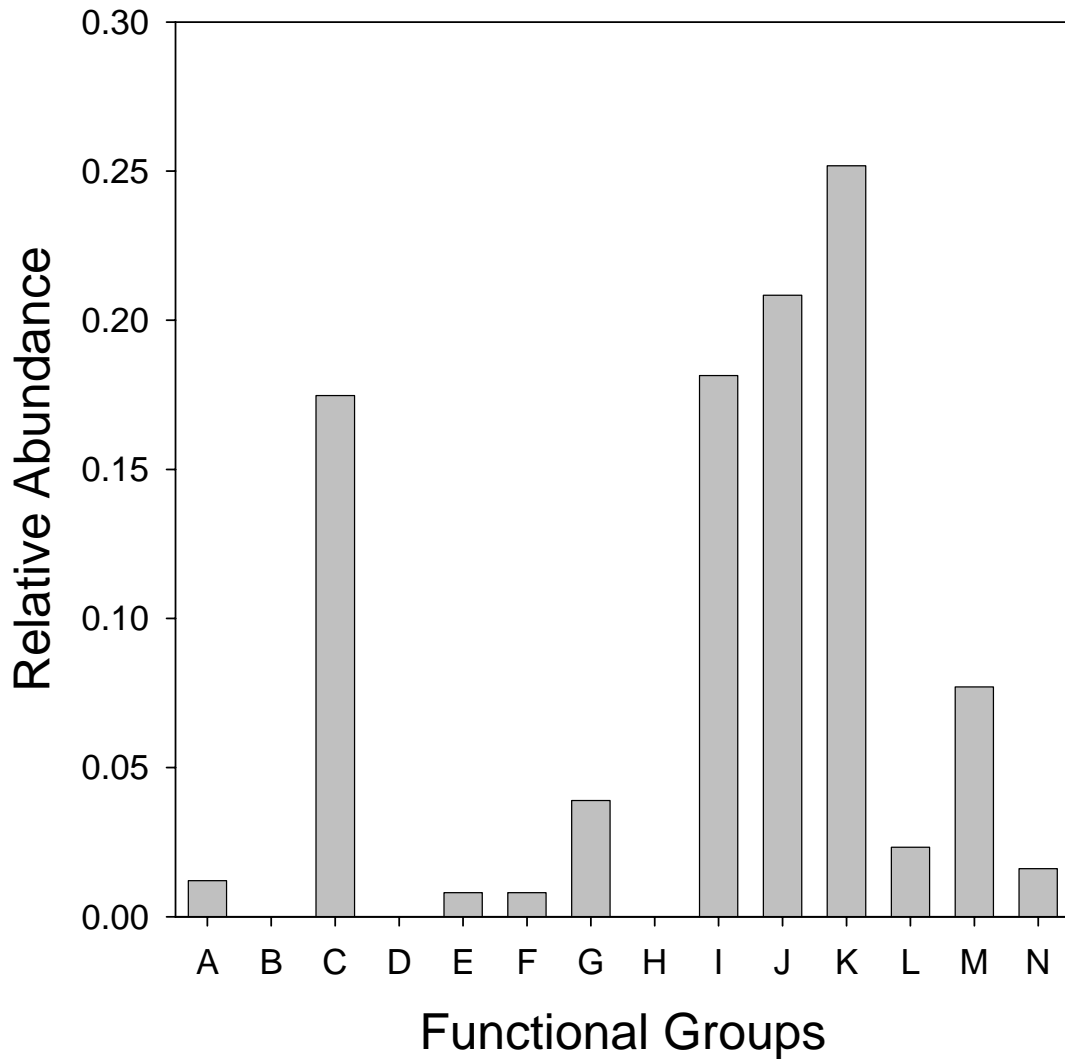


Figure B.9. Functional groupings of stream fish from Catfish Creek, Anderson County, in the Trinity River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

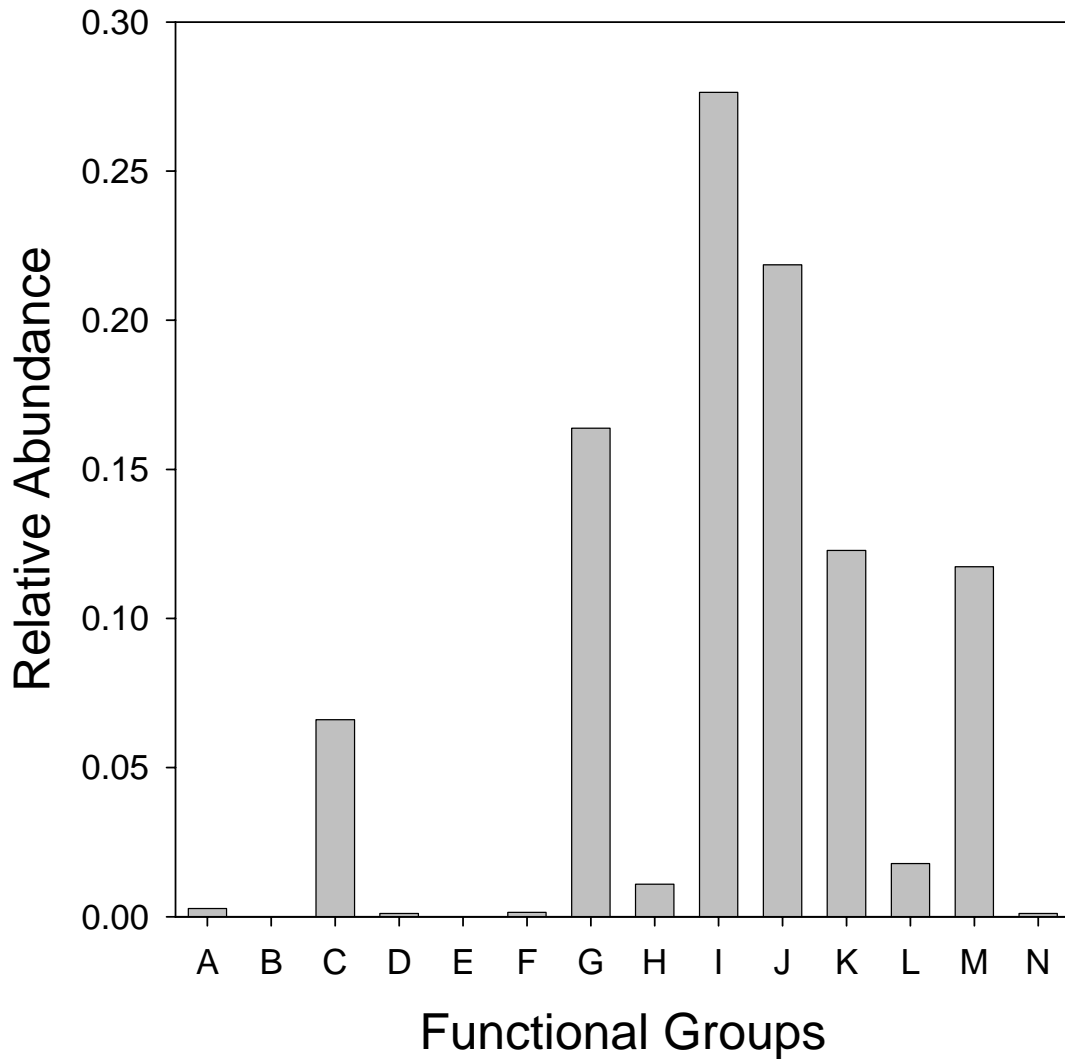


Figure B.10. Functional groupings of stream fish from Big Cypress Creek, Newton County, in the Sabine River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

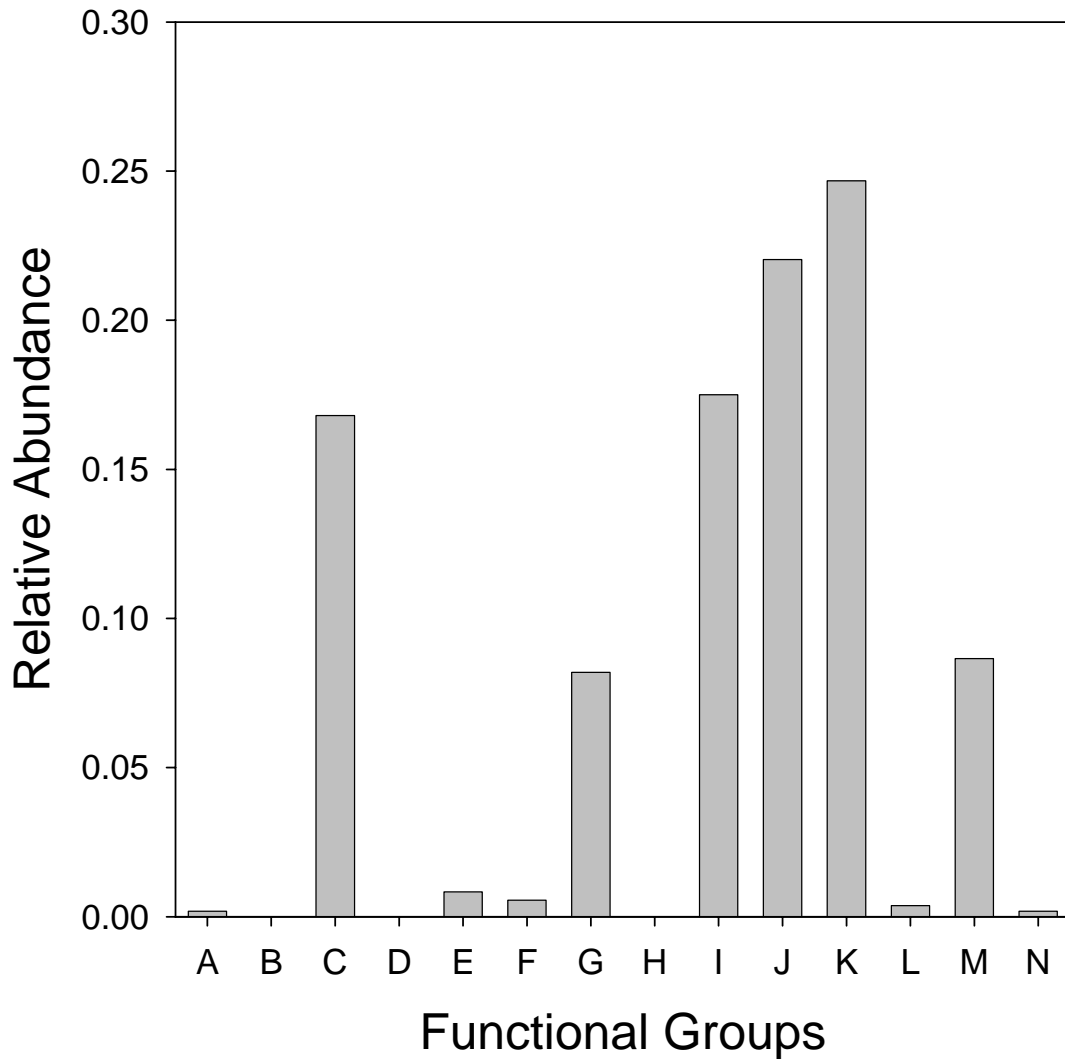


Figure B.11. Functional groupings of stream fish from East Fork of the San Jacinto River, San Jacinto County, in the San Jacinto River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

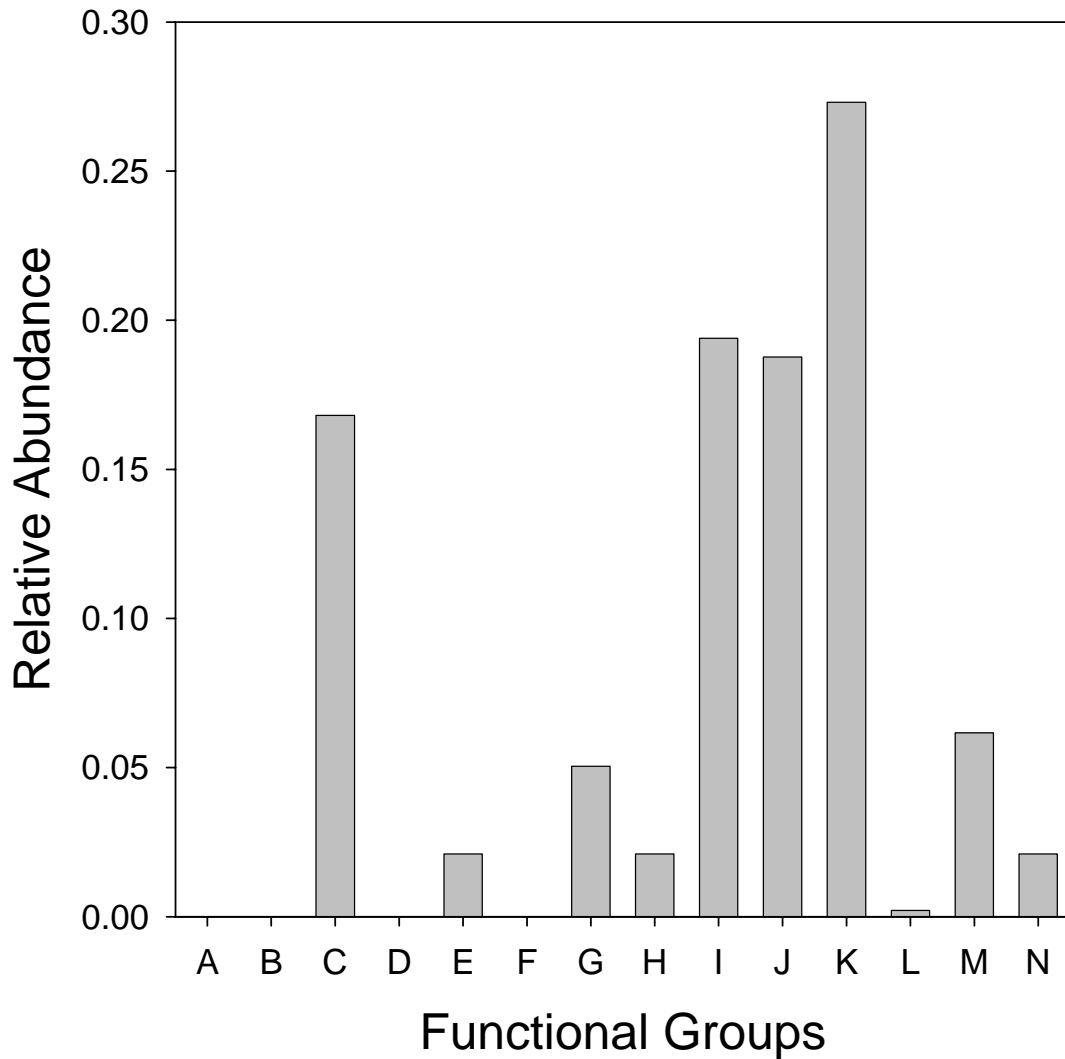


Figure B.12. Functional groupings of stream fish from Keechi Creek, Leon County, in the Trinity River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

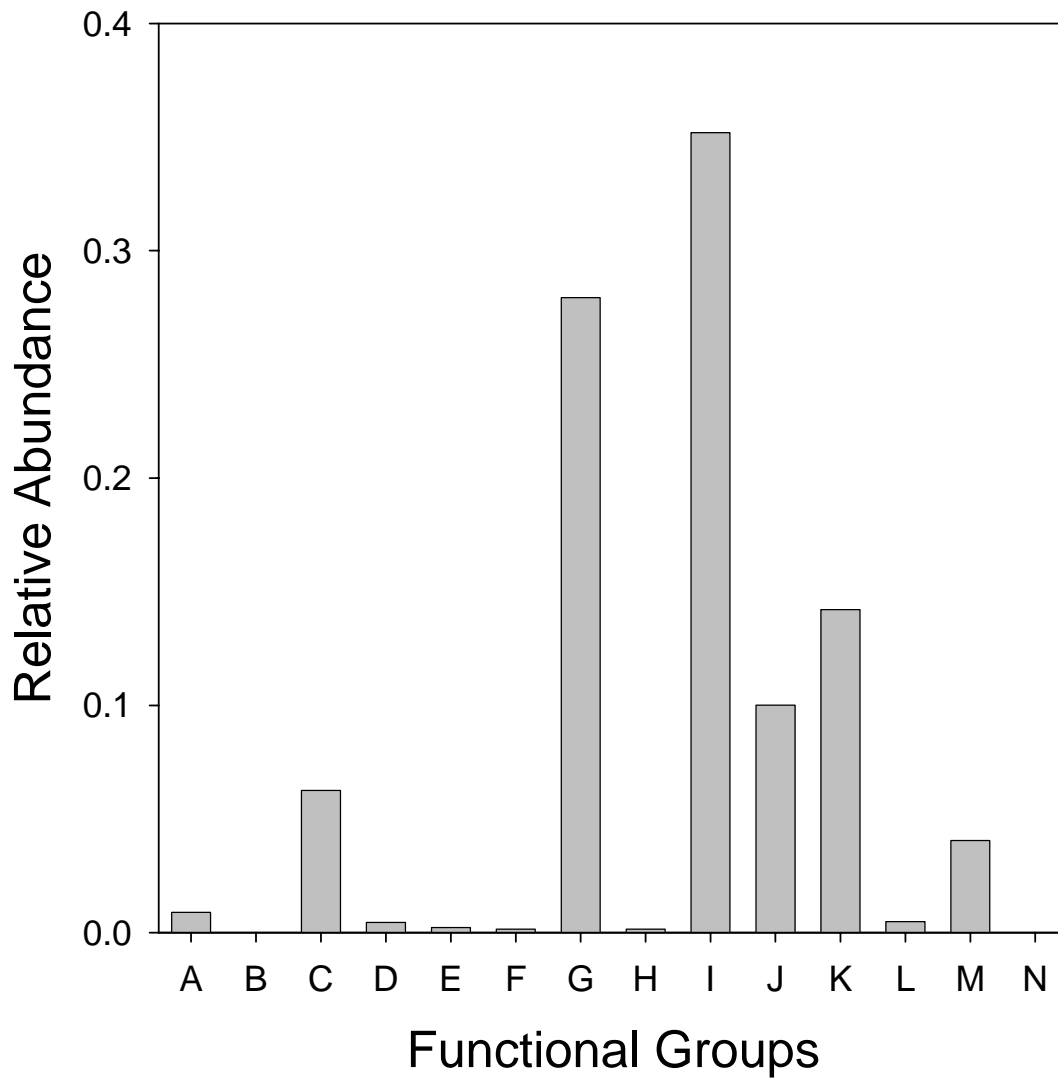


Figure B.13. Functional groupings of stream fish from Piney Creek, Trinity County, in the Neches River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

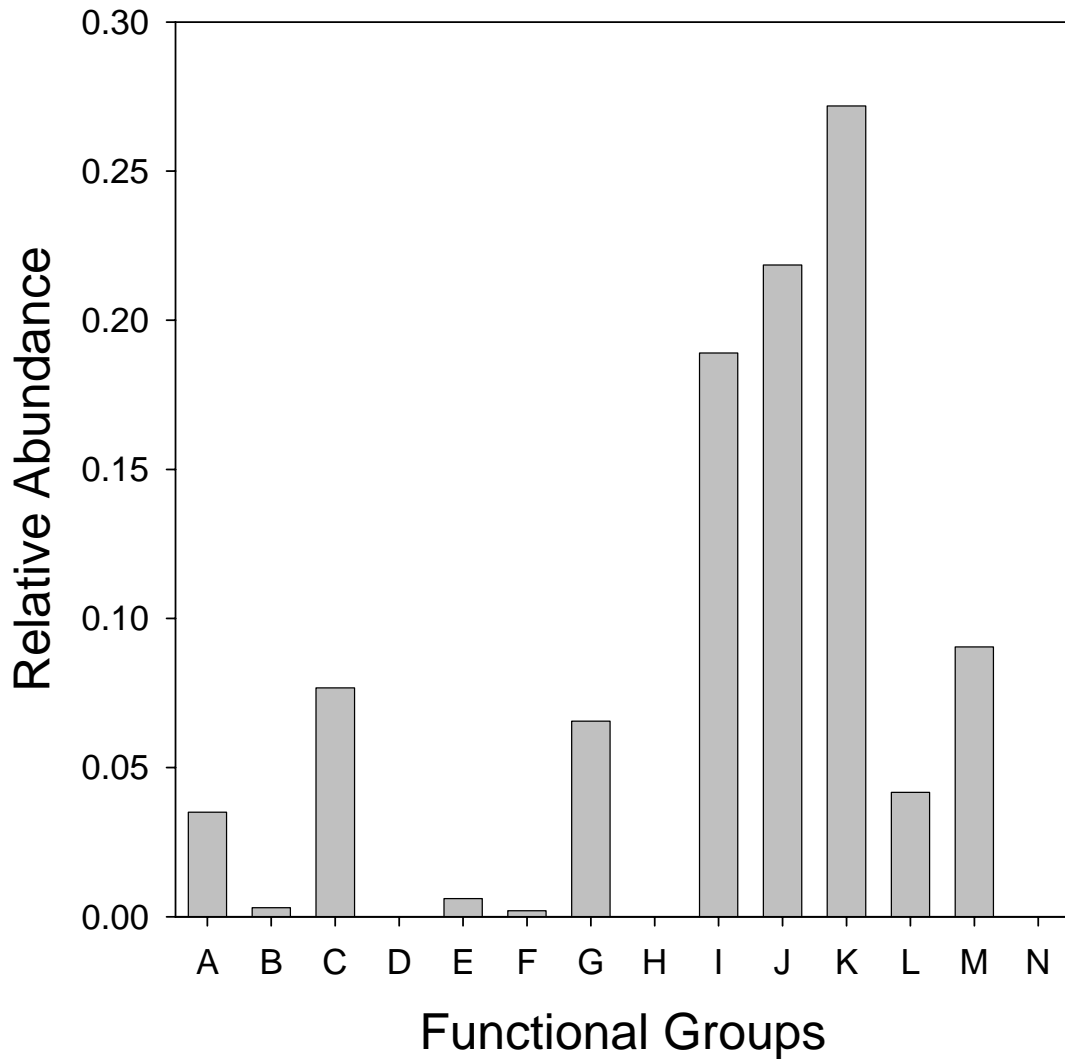


Figure B.14. Functional groupings of stream fish from Irons Bayou, Panola County, in the Sabine River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

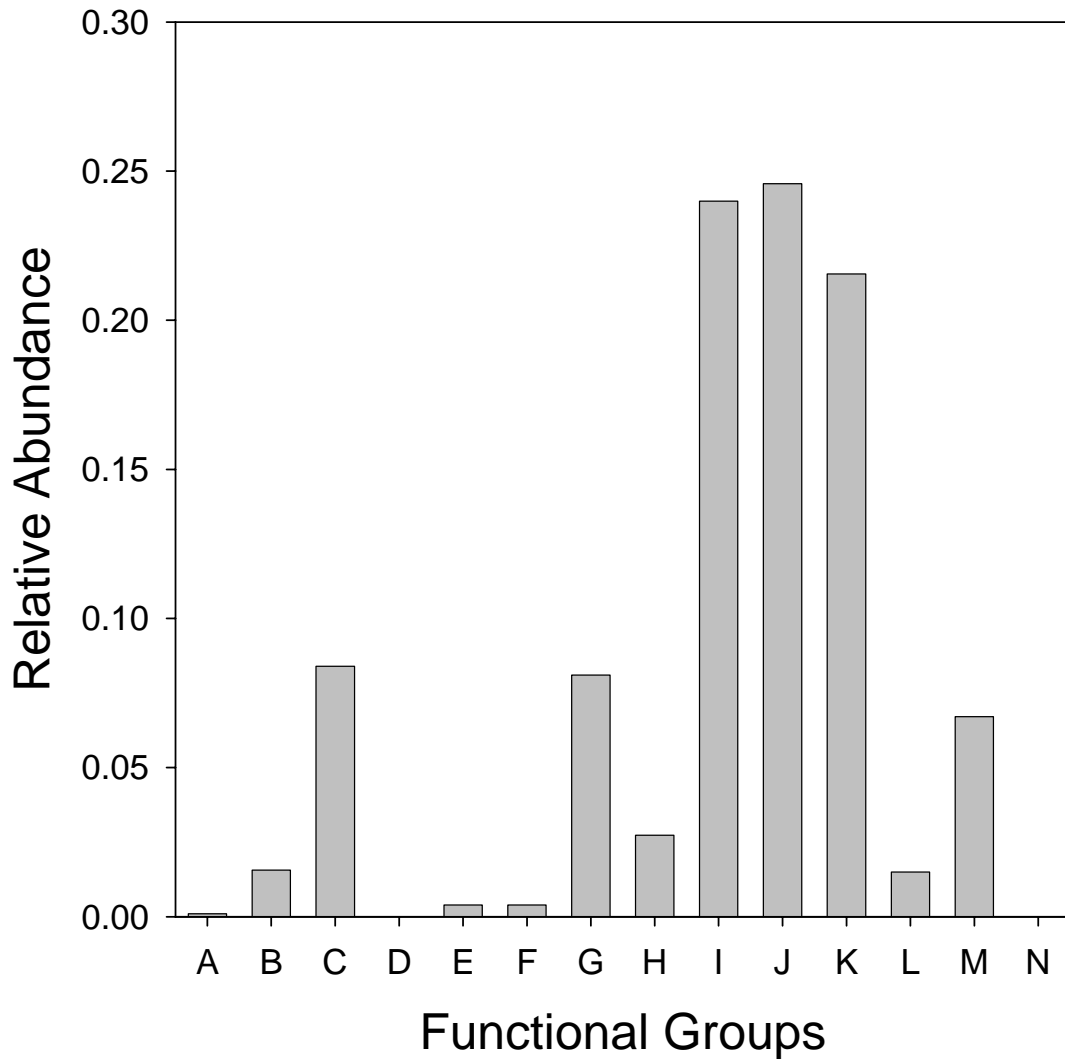


Figure B.15. Functional groupings of stream fish from Frazier Creek, Cass County, in the Cypress River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

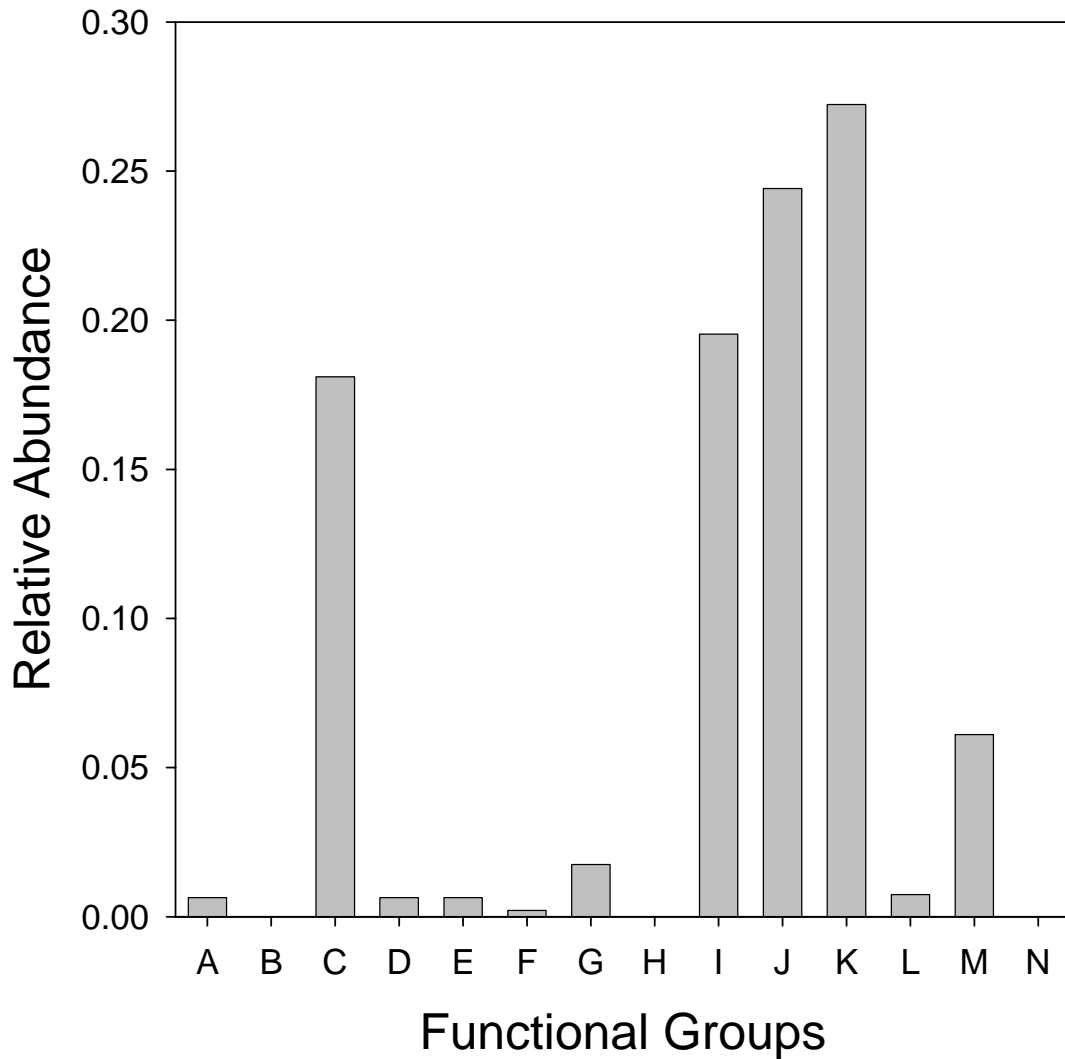


Figure B.16. Functional groupings of stream fish from White Oak Creek, Newton County, in the Sabine River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

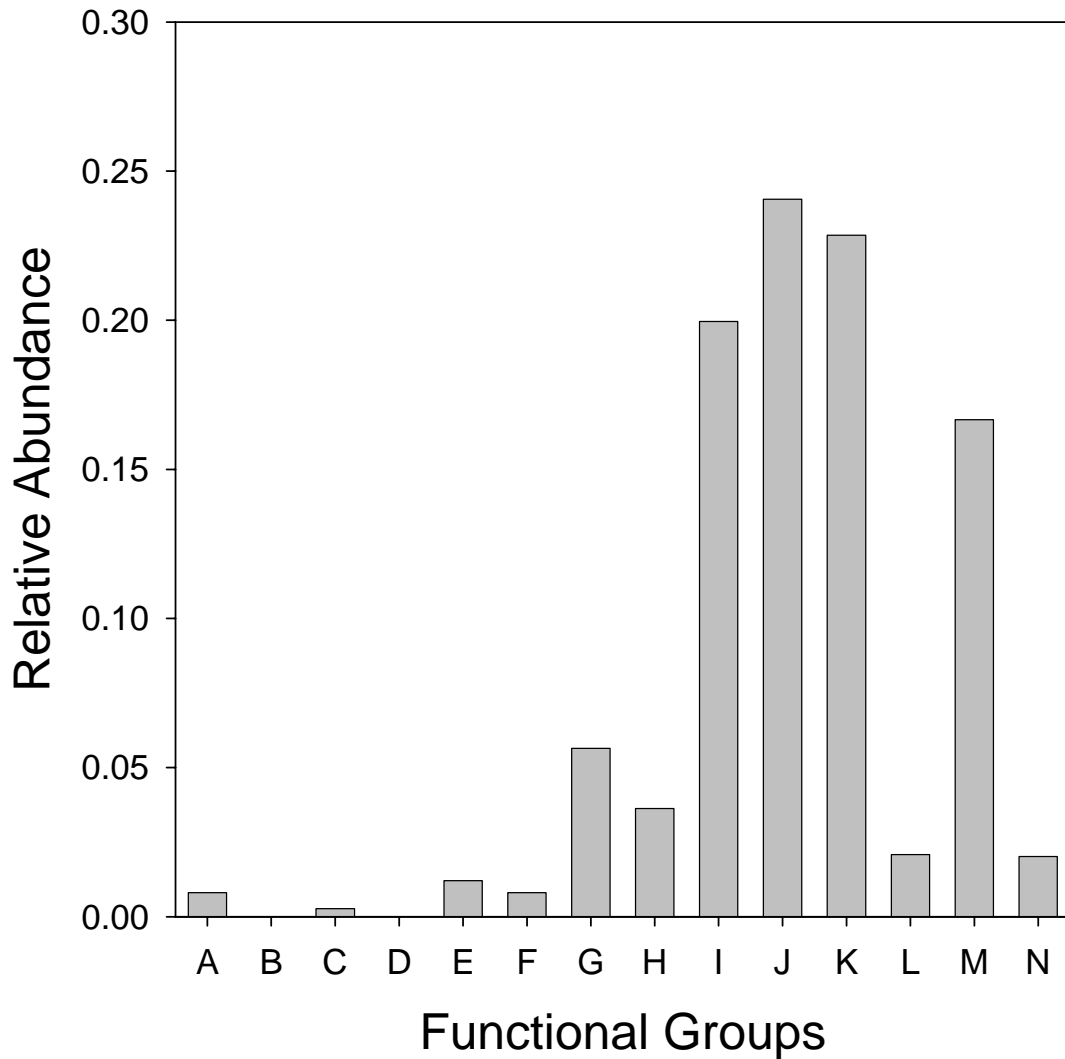


Figure B.17. Functional groupings of stream fish from Beech Creek, Tyler County, in the Neches River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

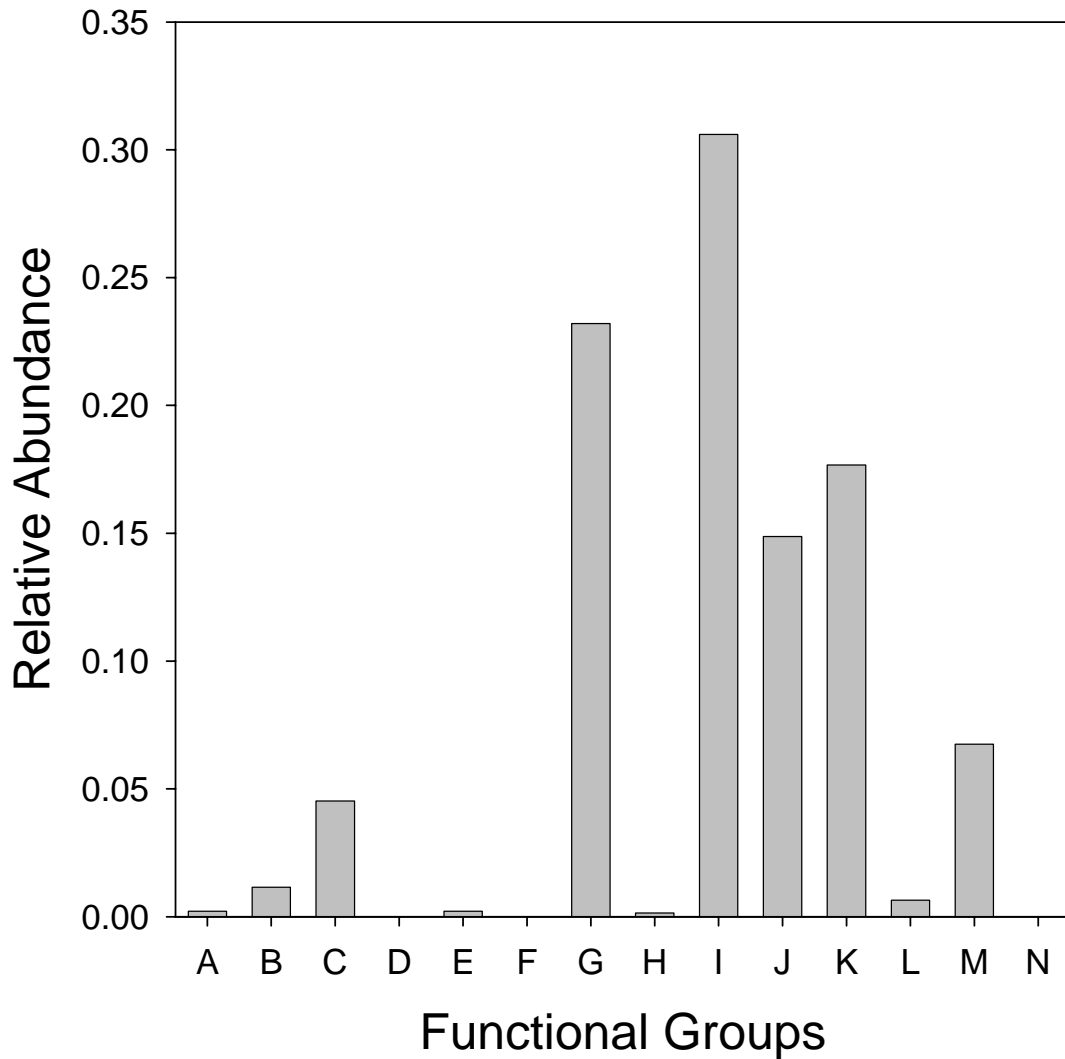


Figure B.18. Functional groupings of stream fish from Black Cypress Creek, Cass County, in the Cypress River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

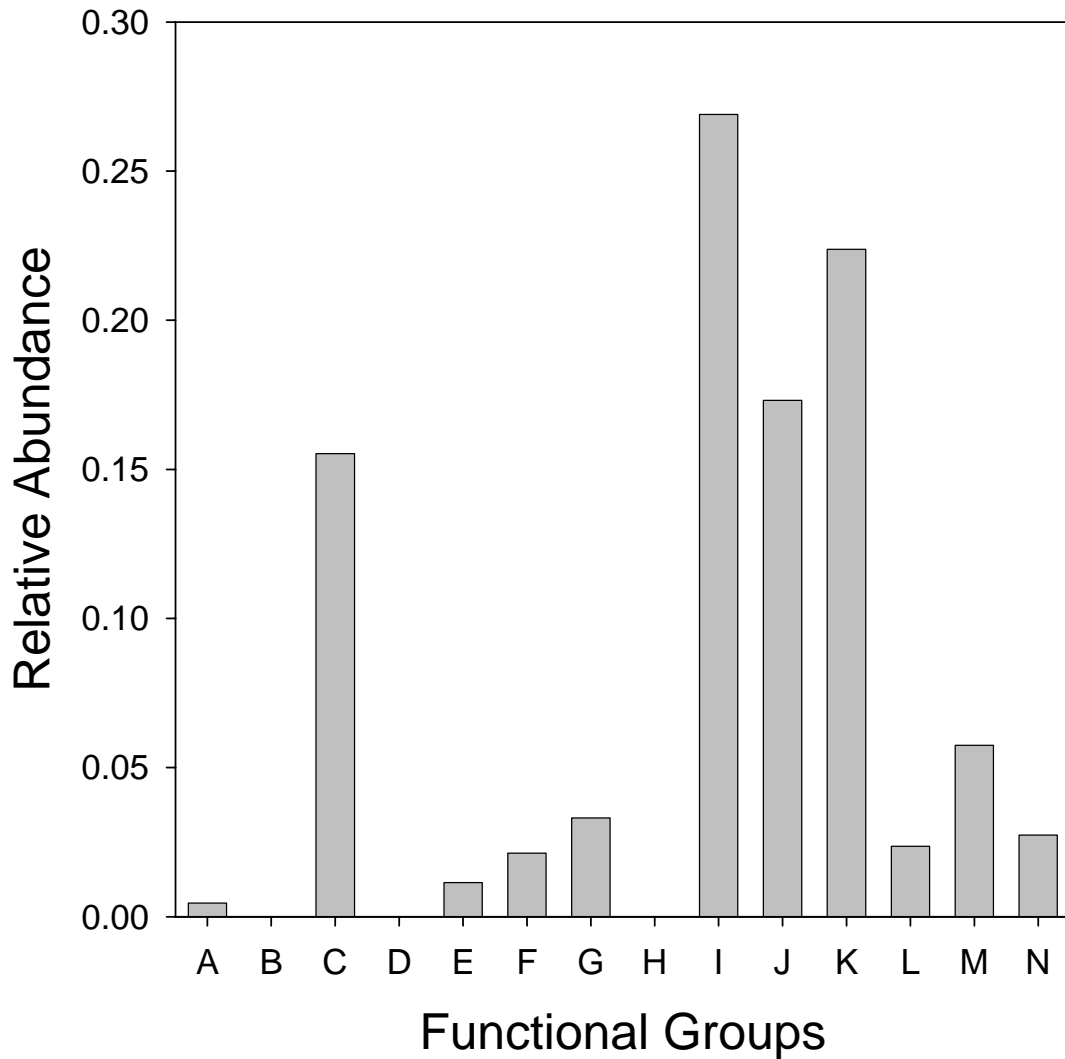


Figure B.19. Functional groupings of stream fish from Wheelock Creek, Leon County, in the Trinity River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

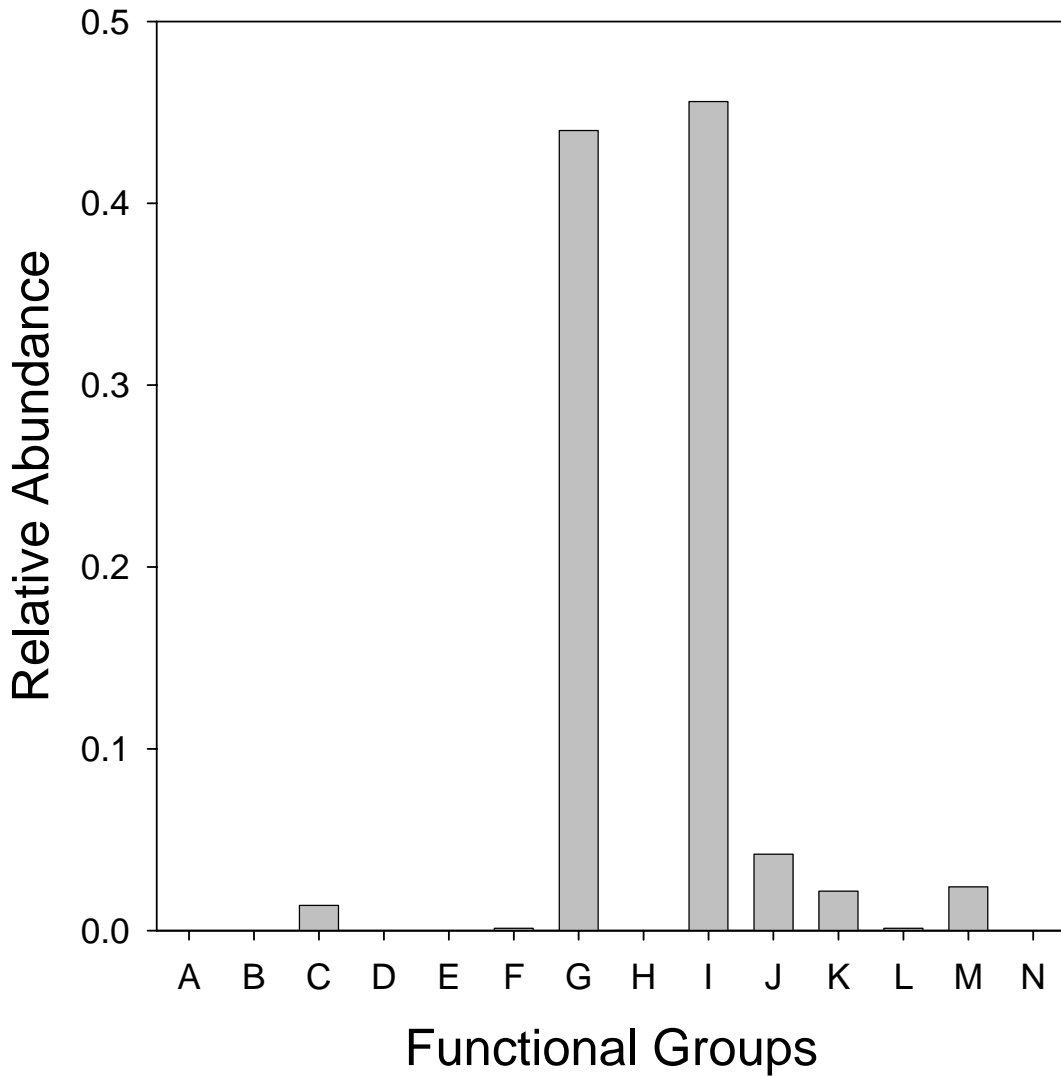


Figure B.20. Functional groupings of stream fish from Ponds Creek, Waller County, in the Brazos River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

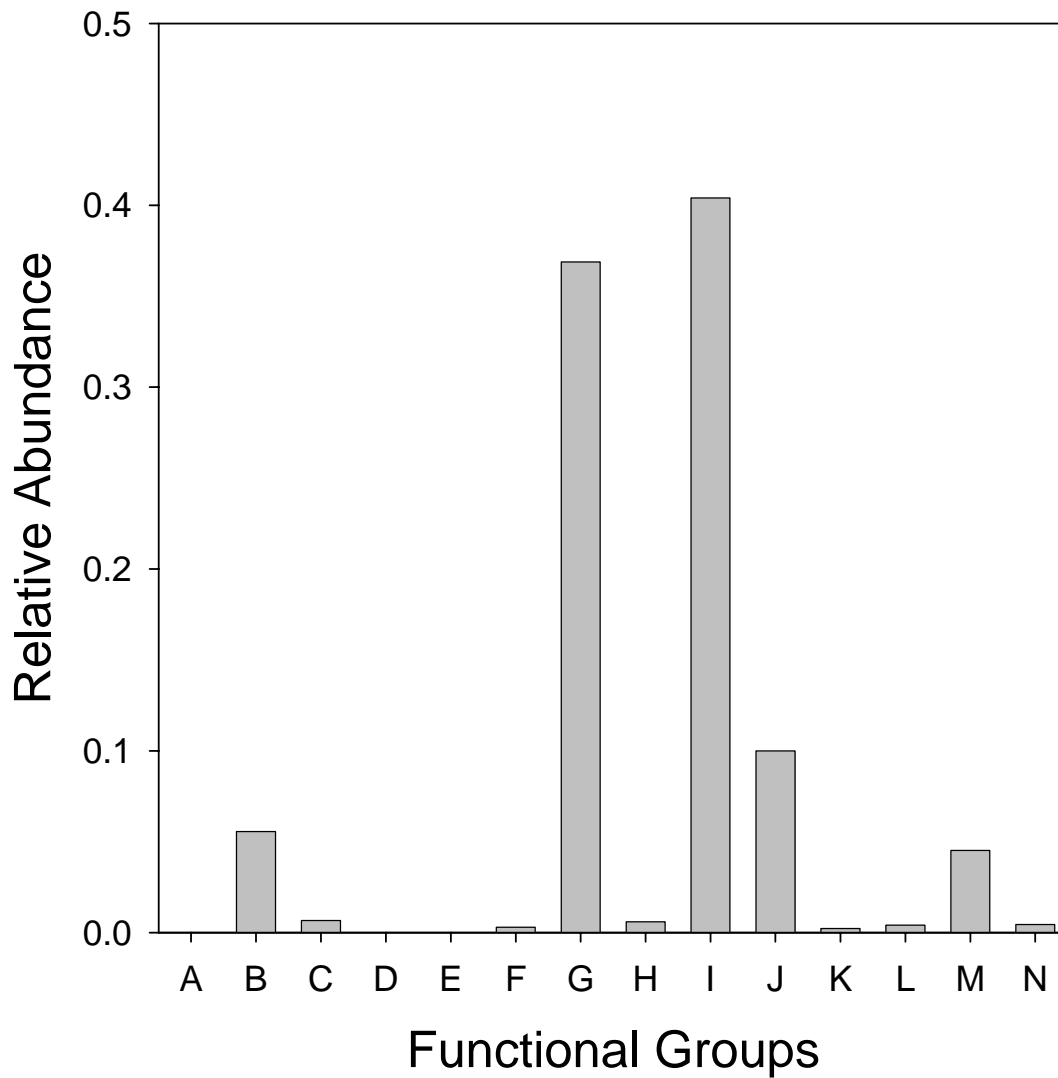


Figure B.21. Functional groupings of stream fish from Sam Miguel Creek, Atascosa County, in the Nueces River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

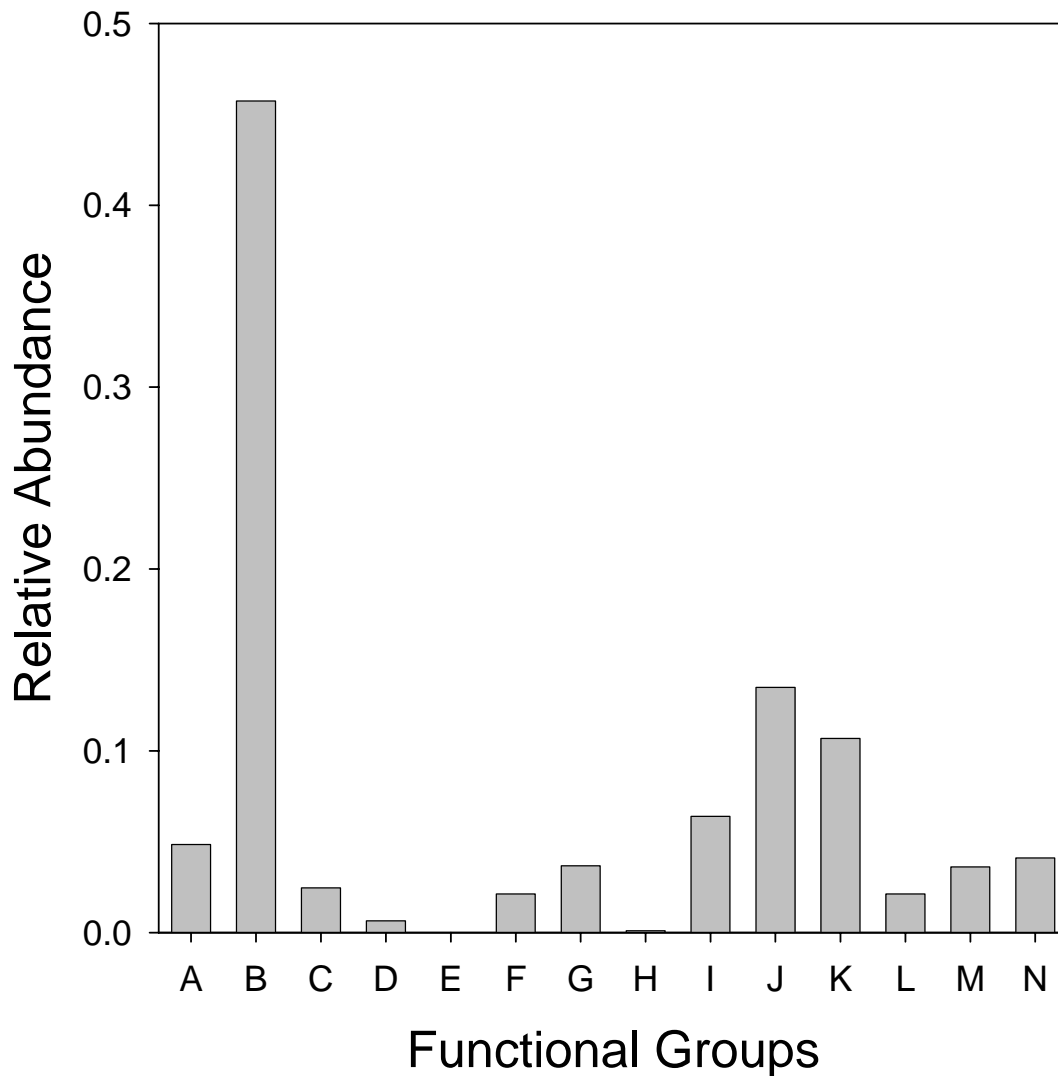


Figure B.22. Functional groupings of stream fish from Sycamore Creek, Kinney County, in the Rio Grande River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

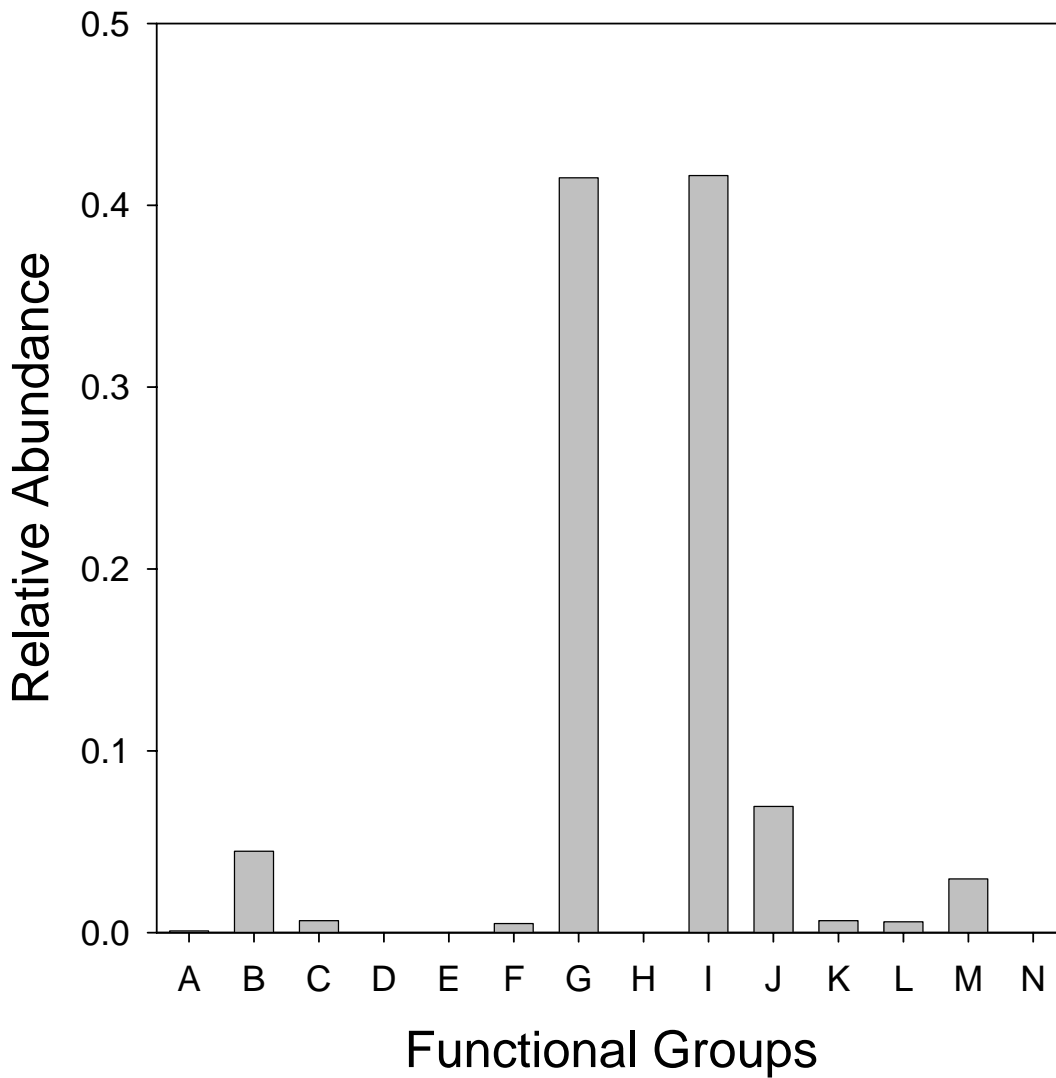


Figure B.23. Functional groupings of stream fish from Metate Creek, Atascosa County, in the Nueces River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

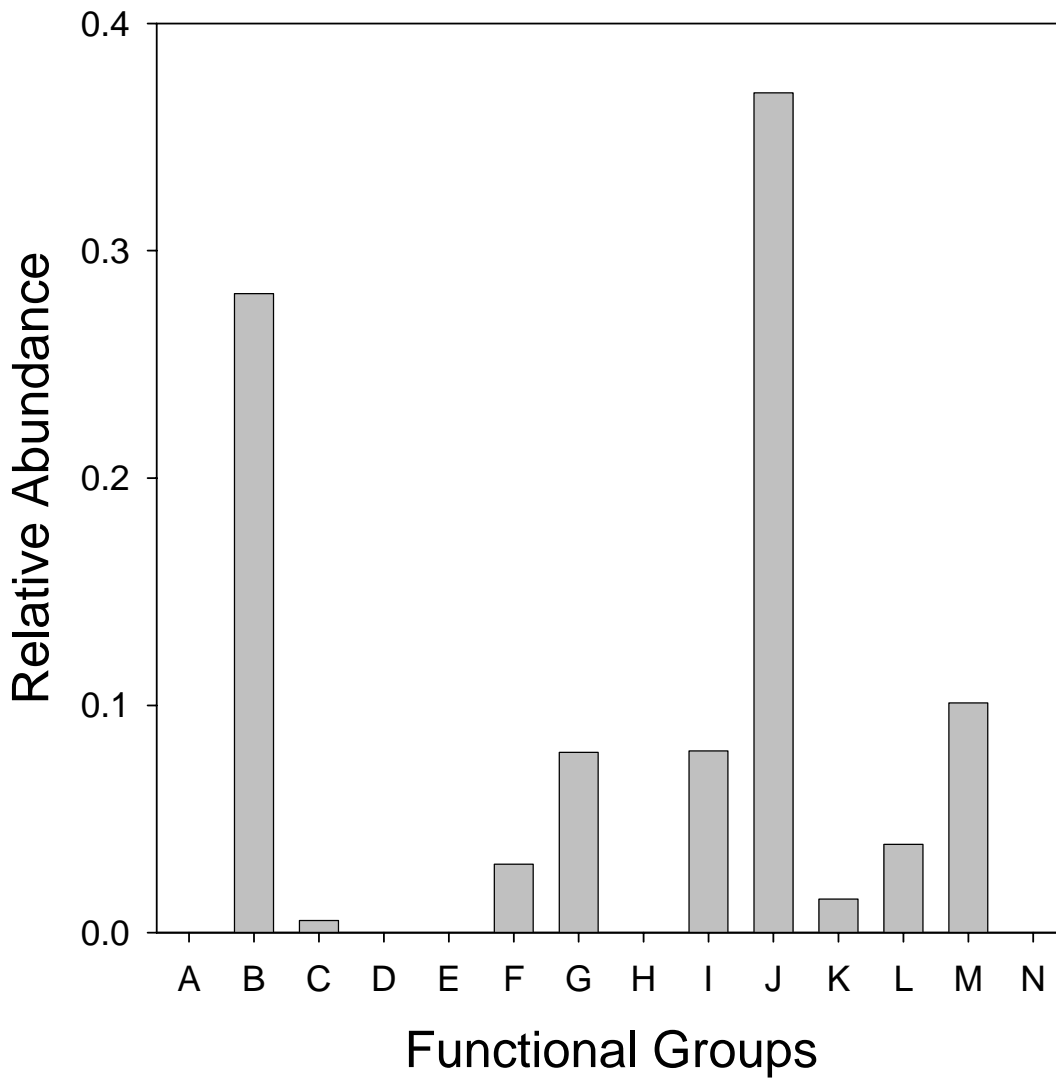


Figure B.24. Functional groupings of stream fish from Pinto Creek, Kinney County, in the Rio Grande River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

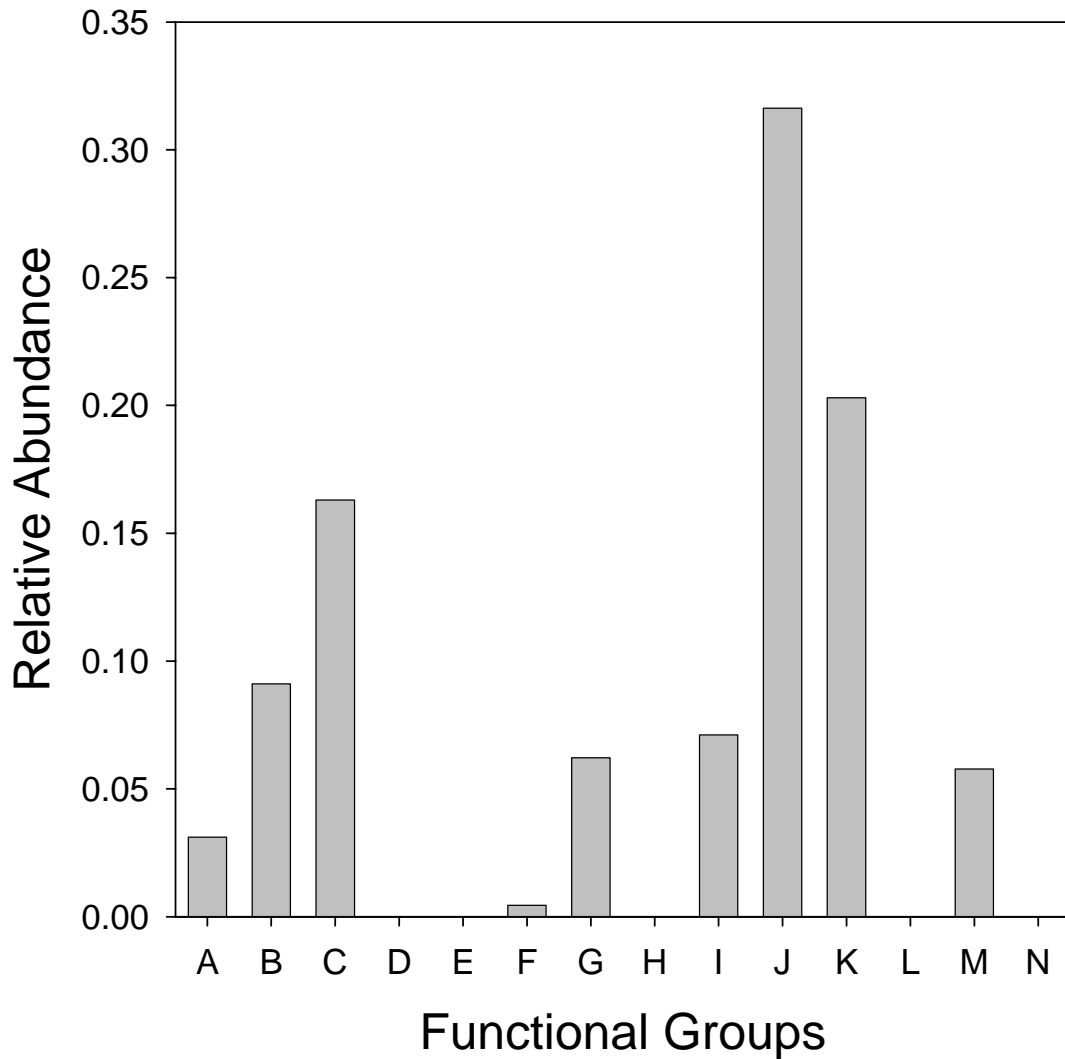


Figure B.25. Functional groupings of stream fish from Cowhouse Creek, Coryell County, in the Brazos River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

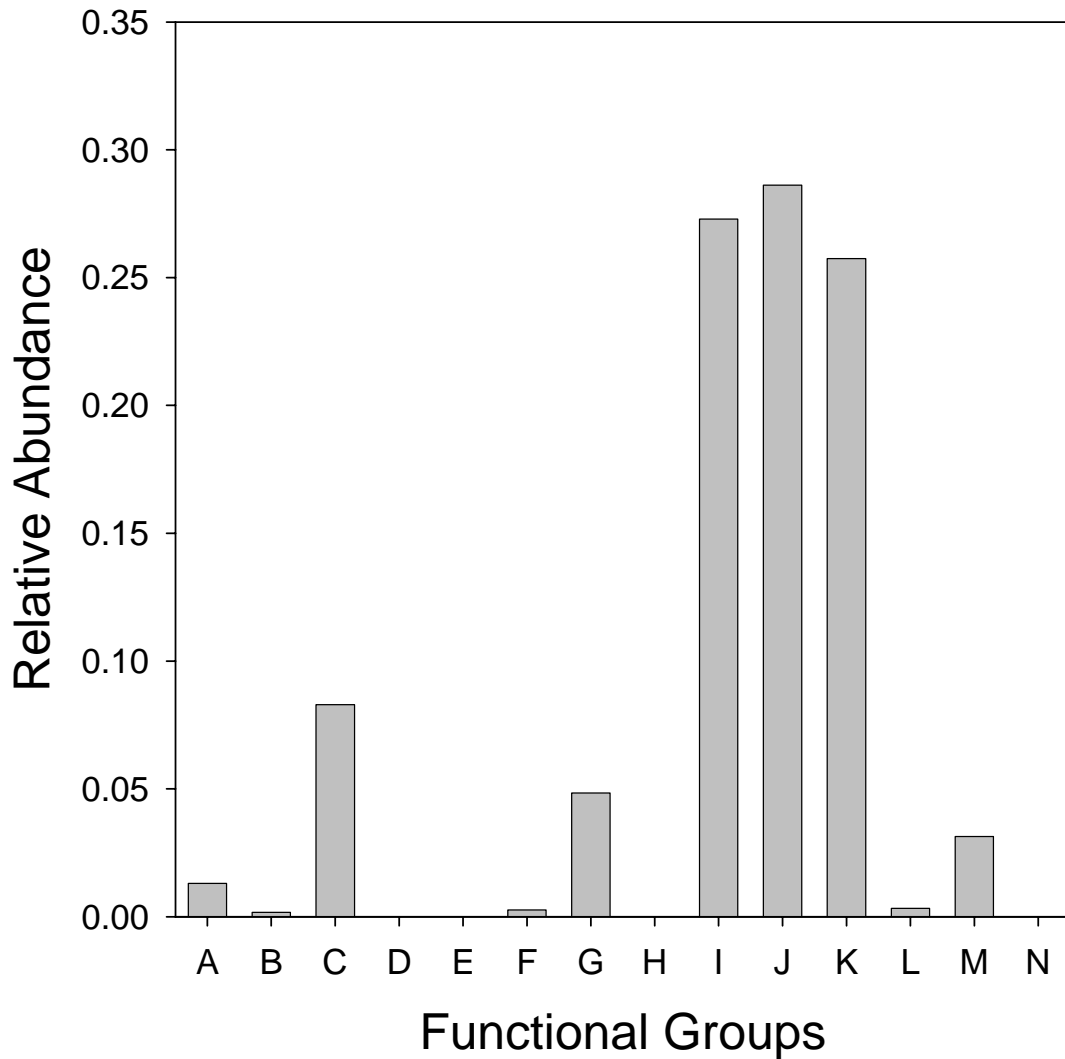


Figure B.26. Functional groupings of stream fish from Medina River, Bandera County, in the San Antonio River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

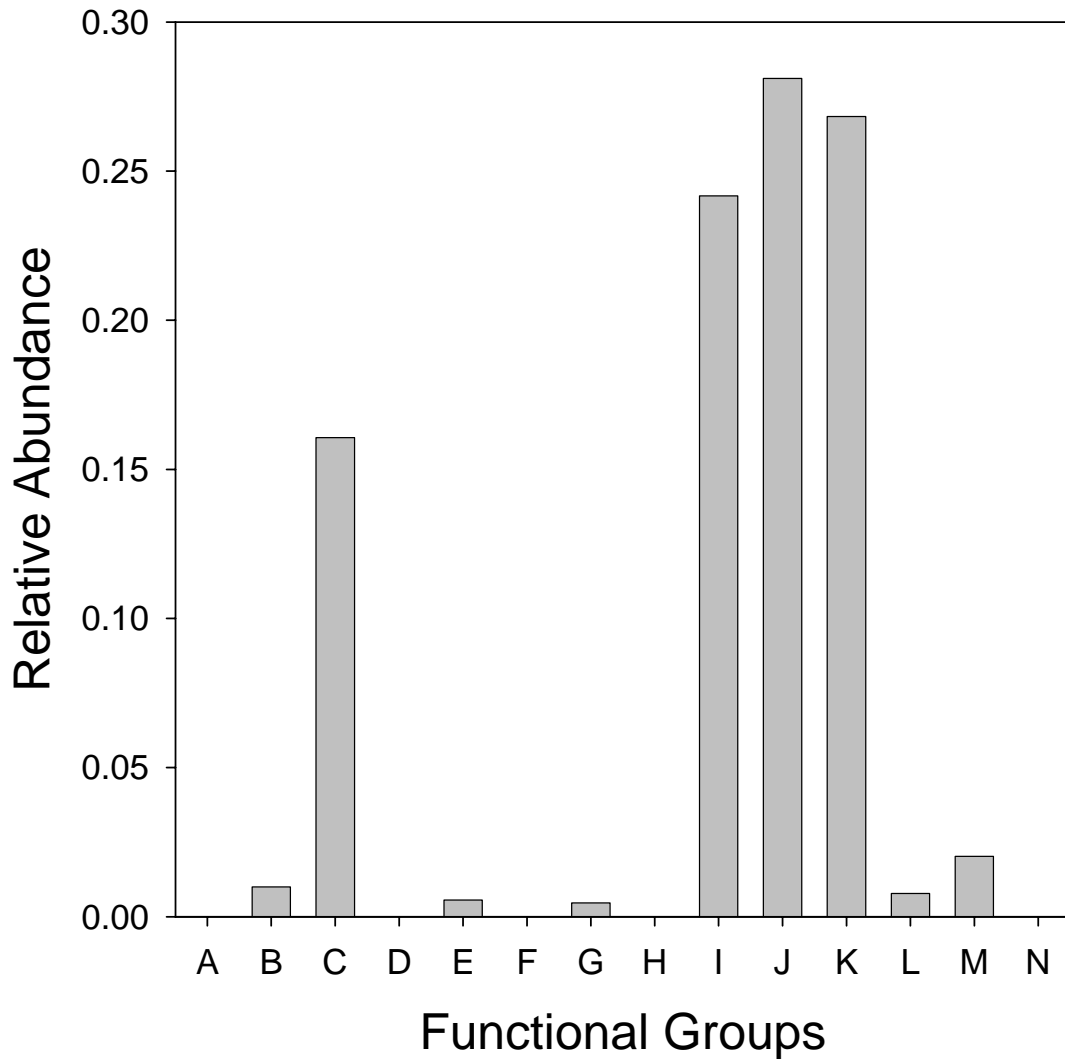


Figure B.27. Functional groupings of stream fish from South Llano River, Kimble County, in the Colorado River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

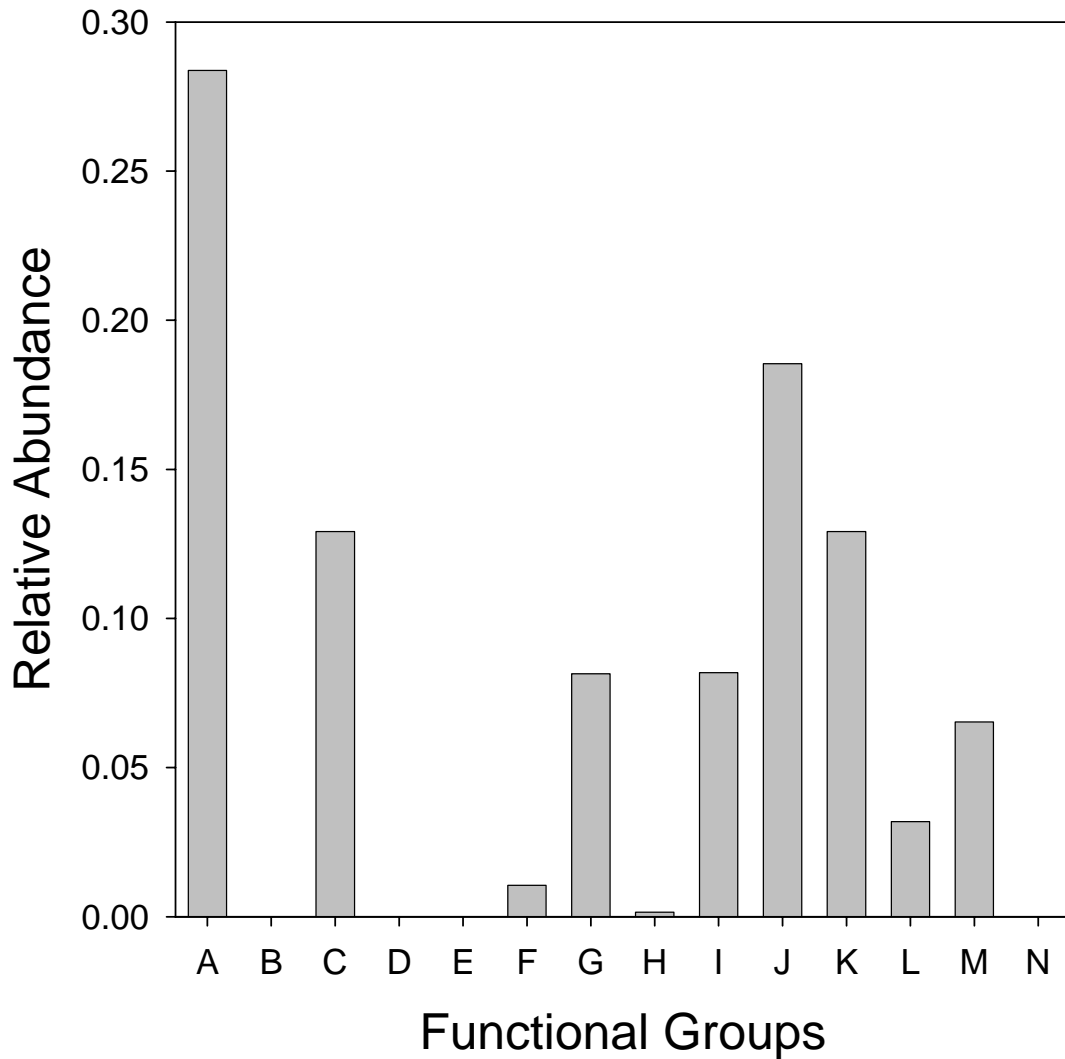


Figure B.28. Functional groupings of stream fish from Onion Creek, Hays County, in the Colorado River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

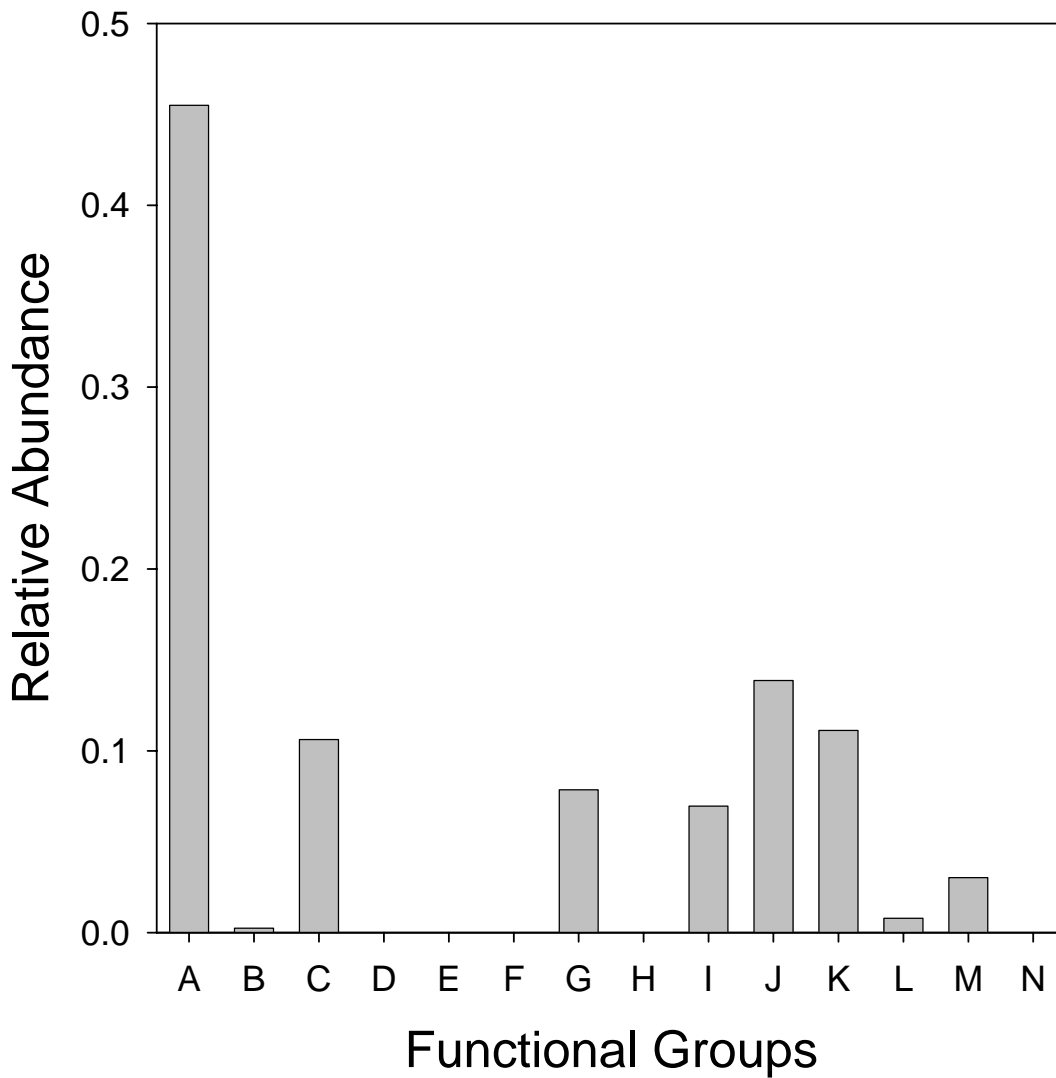


Figure B.29. Functional groupings of stream fish from Rocky Creek, Burnet County, in the Brazos River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

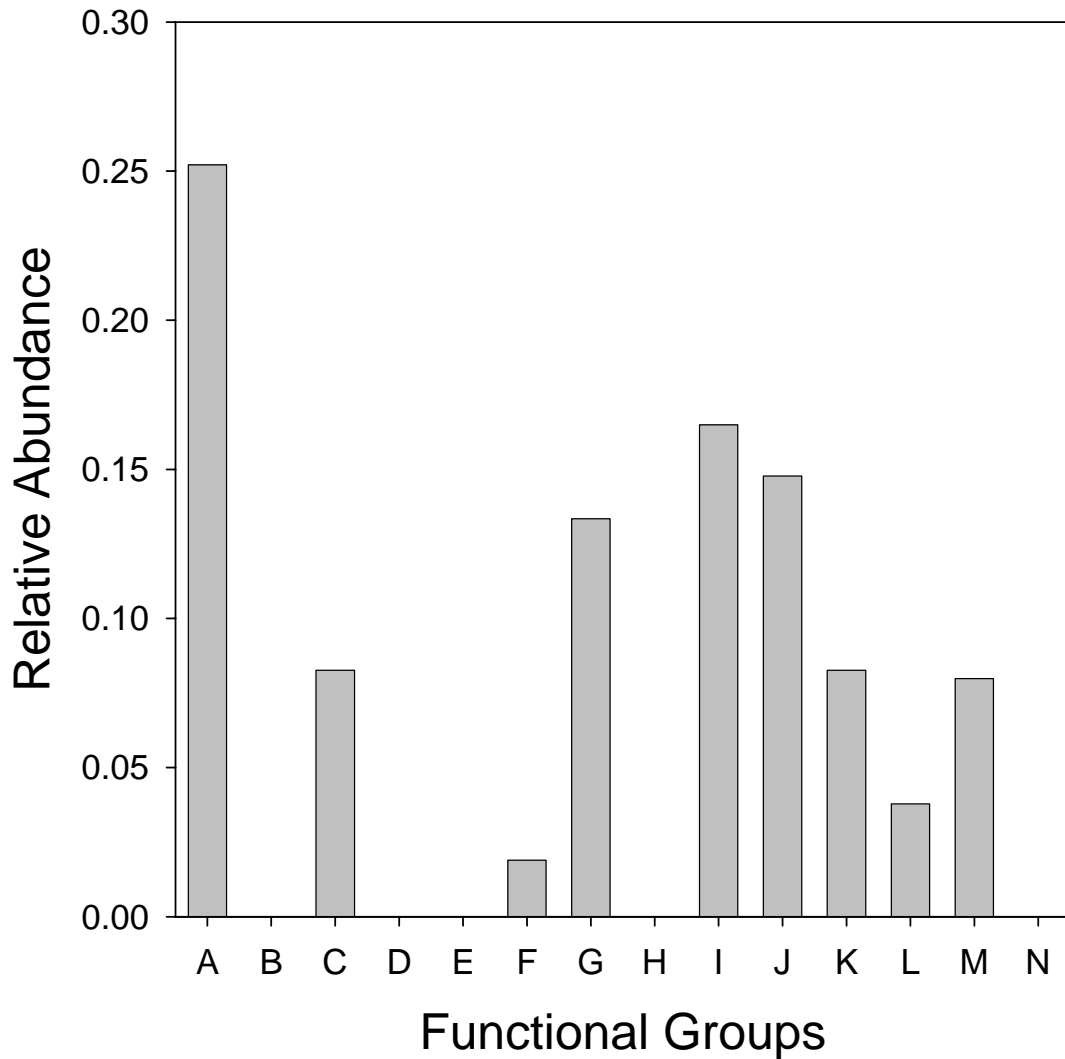


Figure B.30. Functional groupings of stream fish from Barton Creek, Travis County, in the Colorado River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

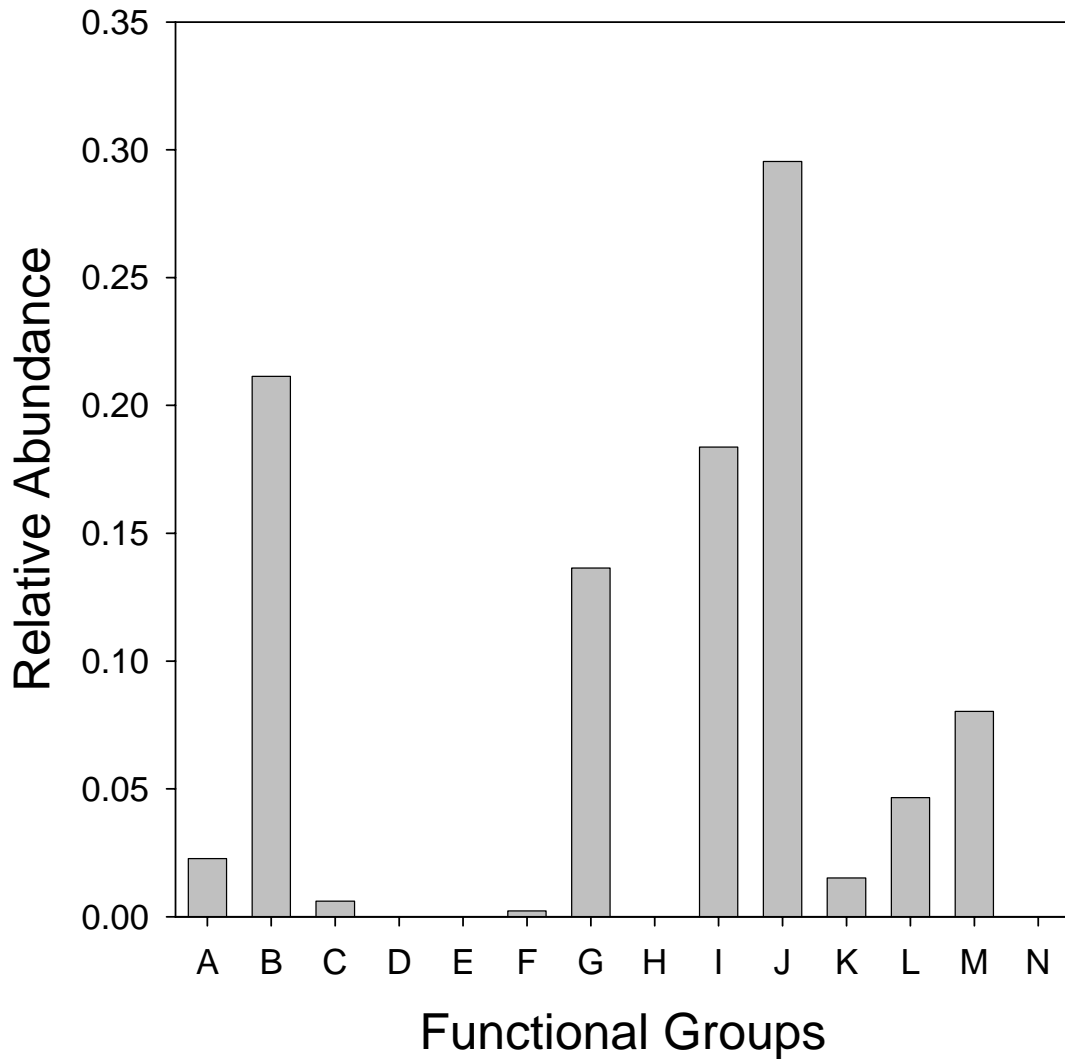


Figure B.31. Functional groupings of stream fish from Little Blanco River, Blanco County, in the Guadalupe River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

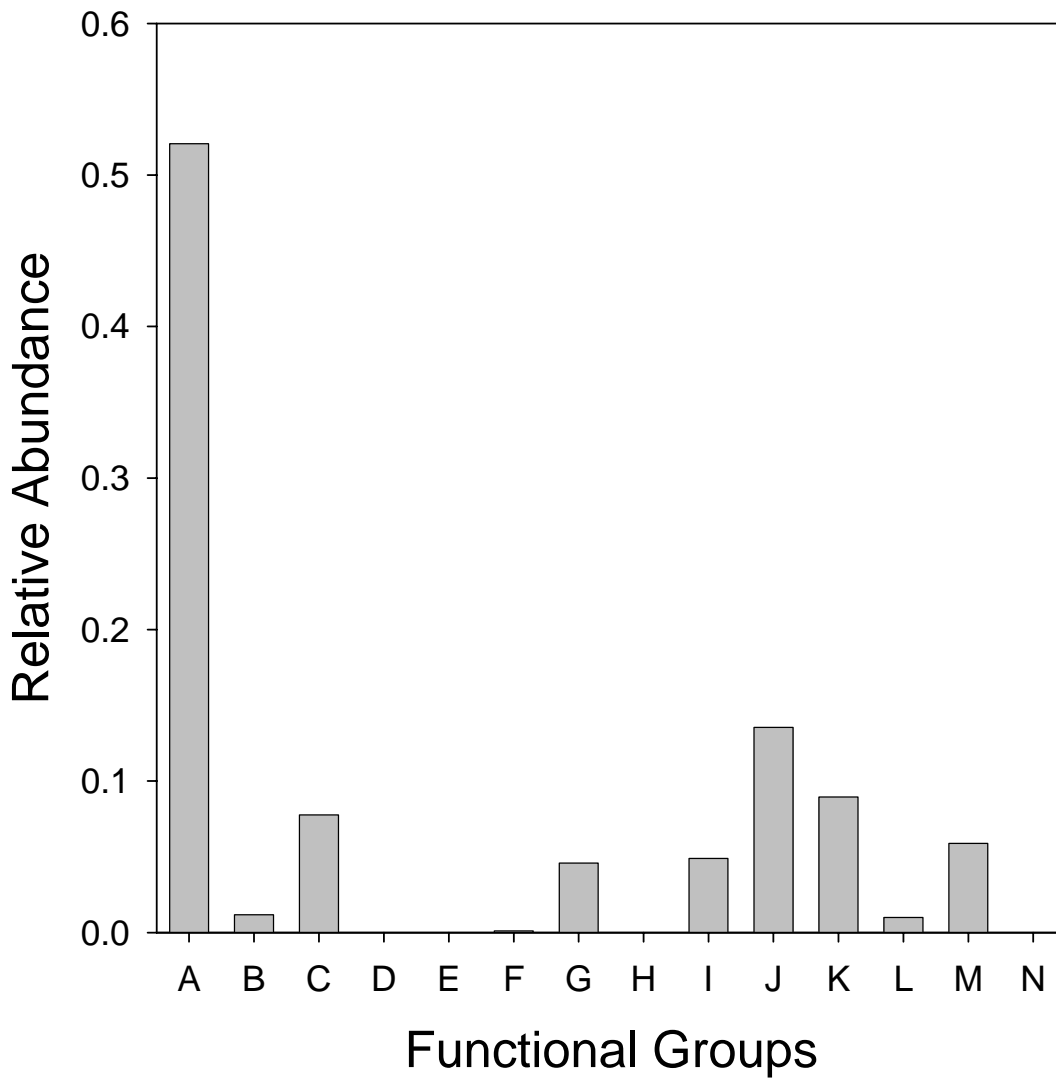


Figure B.32. Functional groupings of stream fish from Oatmeal Creek, Burnet County, in the Brazos River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

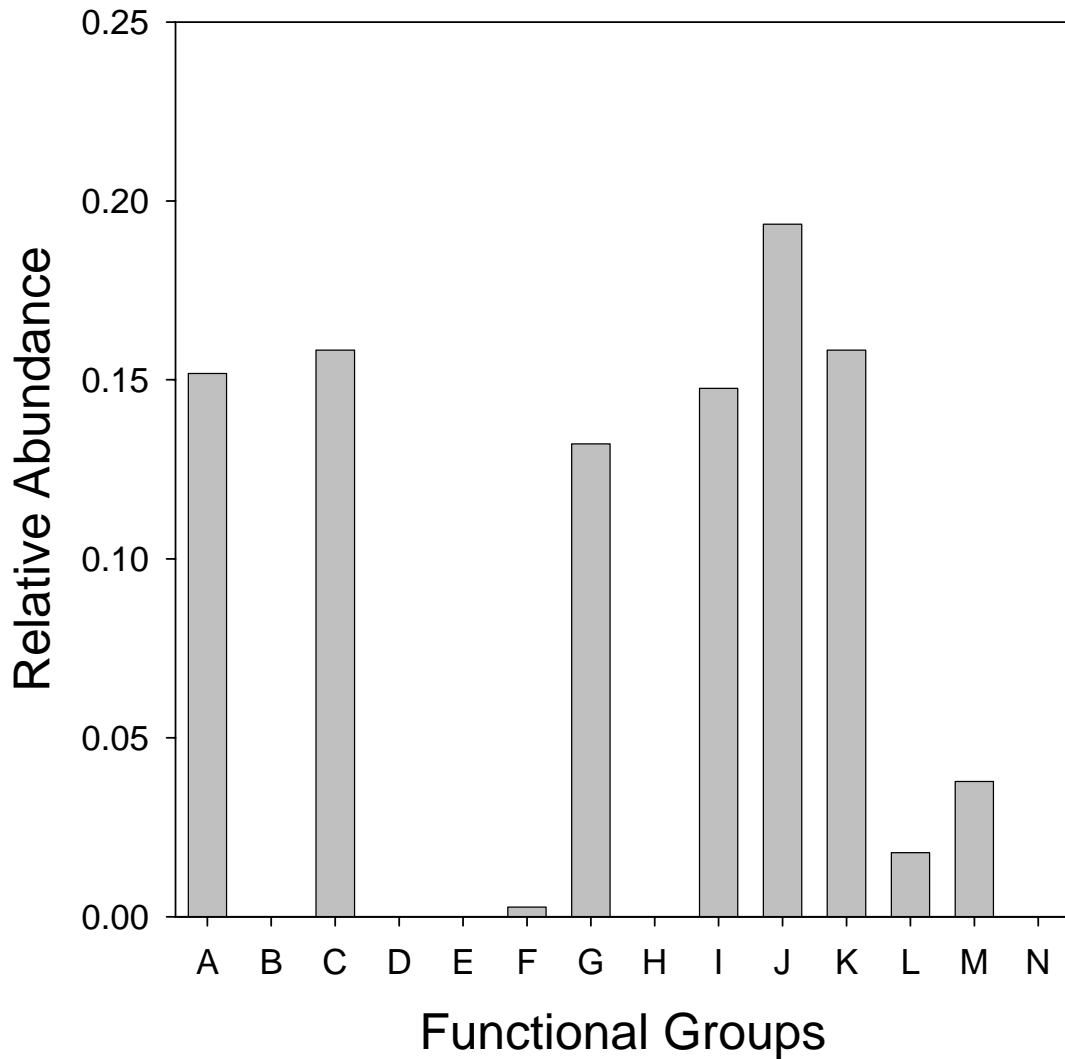


Figure B.33. Functional groupings of stream fish from Little Barton Creek, Travis County, in the Colorado River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

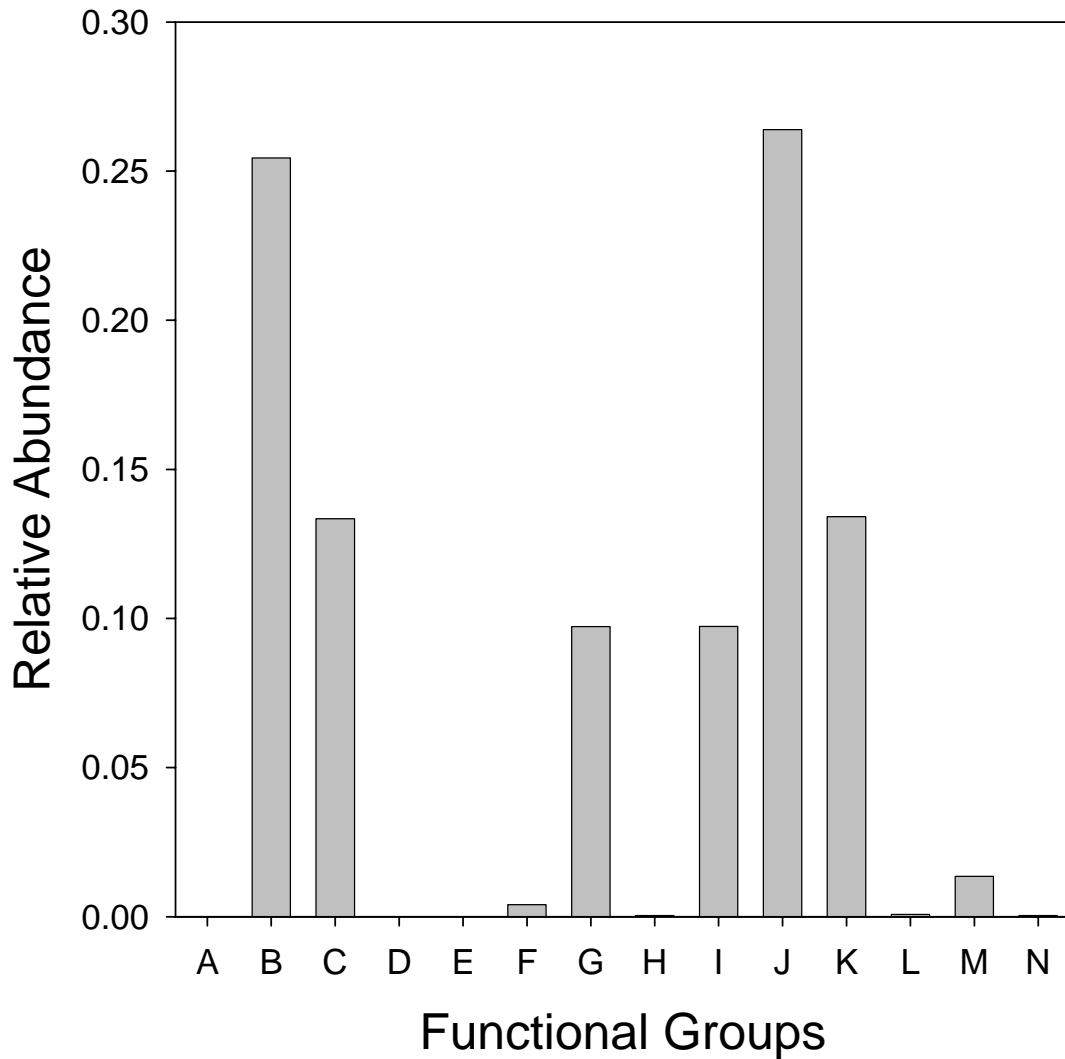


Figure B.34. Functional groupings of stream fish from Elm Creek, Runnels County, in the Colorado River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

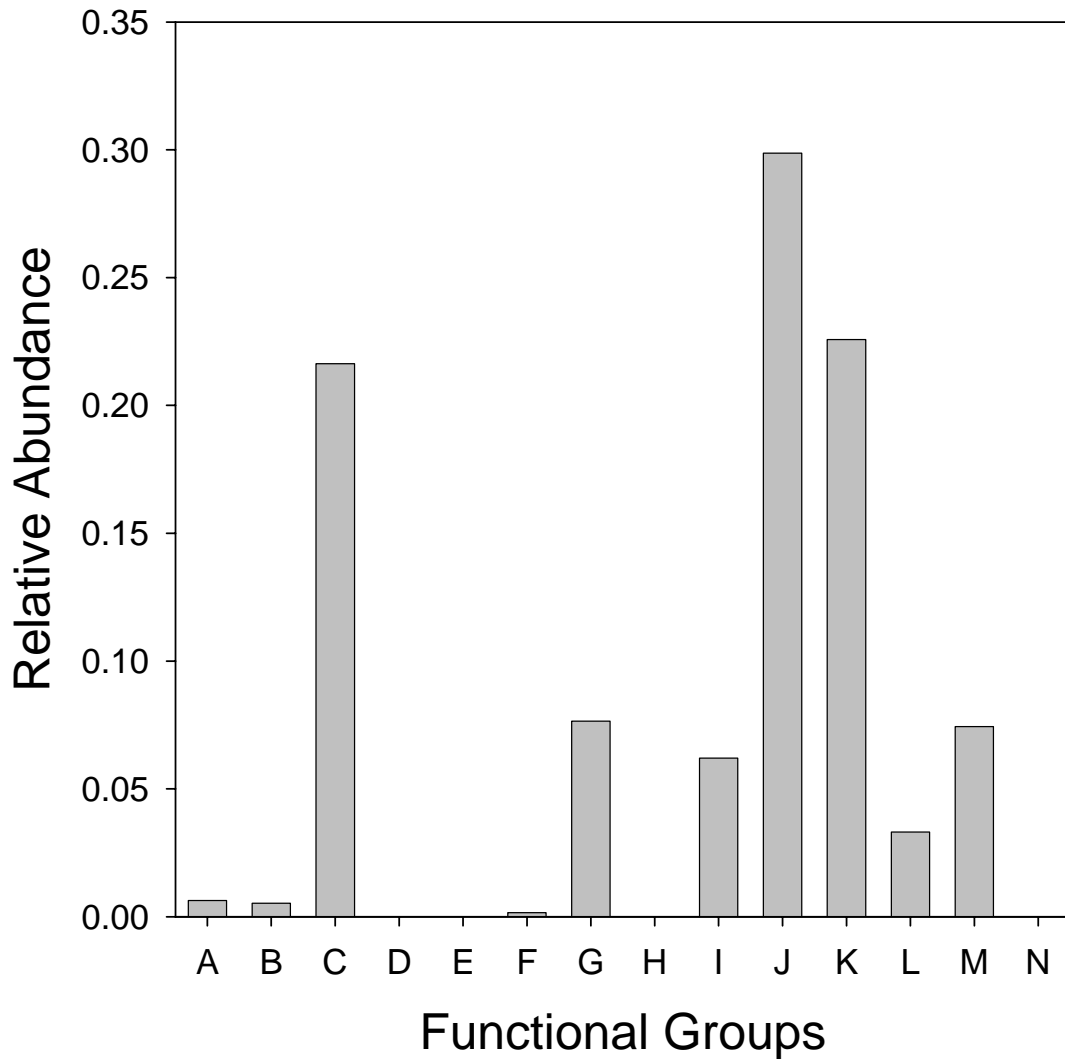


Figure B.35. Functional groupings of stream fish from Spring Creek, Irion County, in the Colorado River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

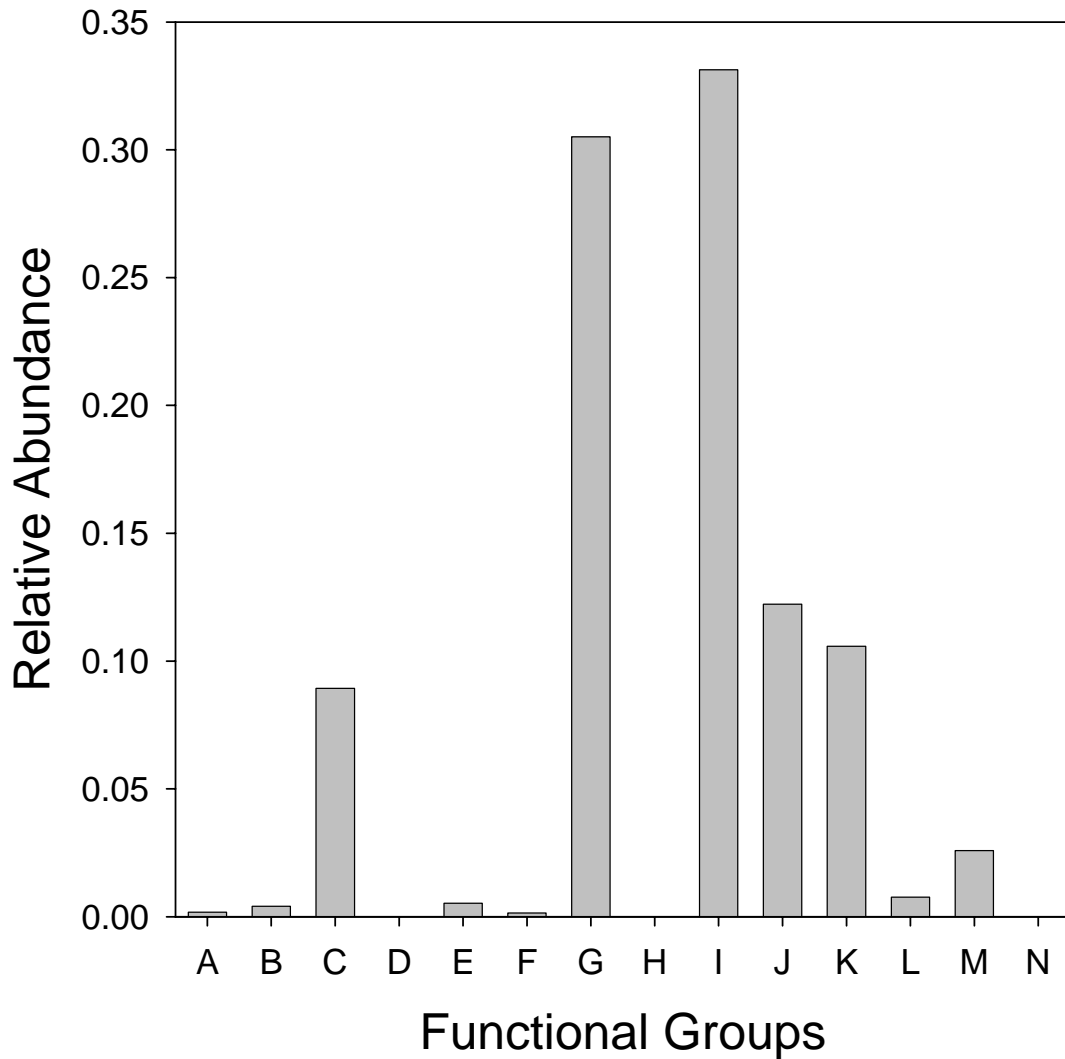


Figure B.36. Functional groupings of stream fish from Cummings Creek, Colorado County, in the Colorado River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

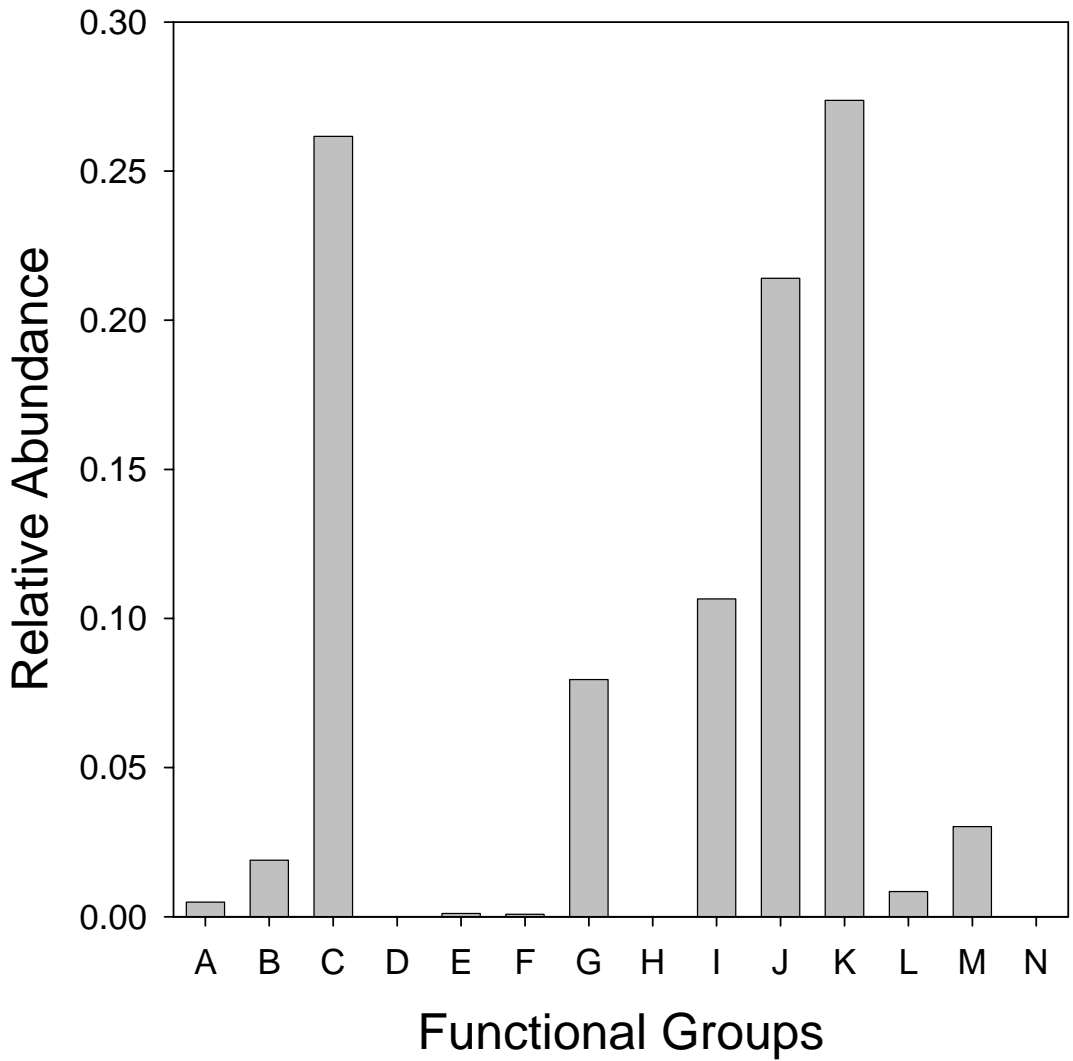


Figure B.37. Functional groupings of stream fish from Mill Creek, Austin County, in the Brazos River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

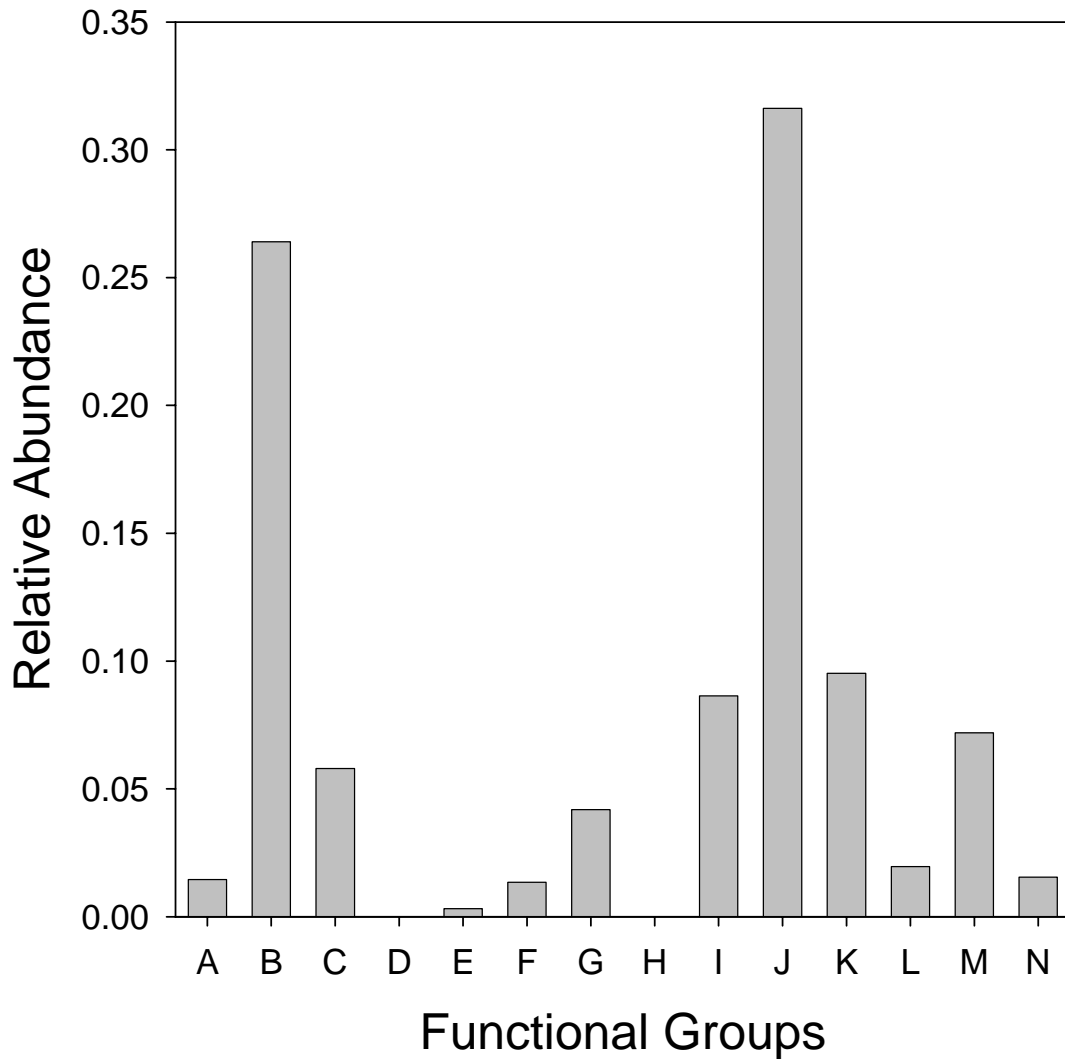


Figure B.38. Functional groupings of stream fish from Clear Creek, Denton County, in the Trinity River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

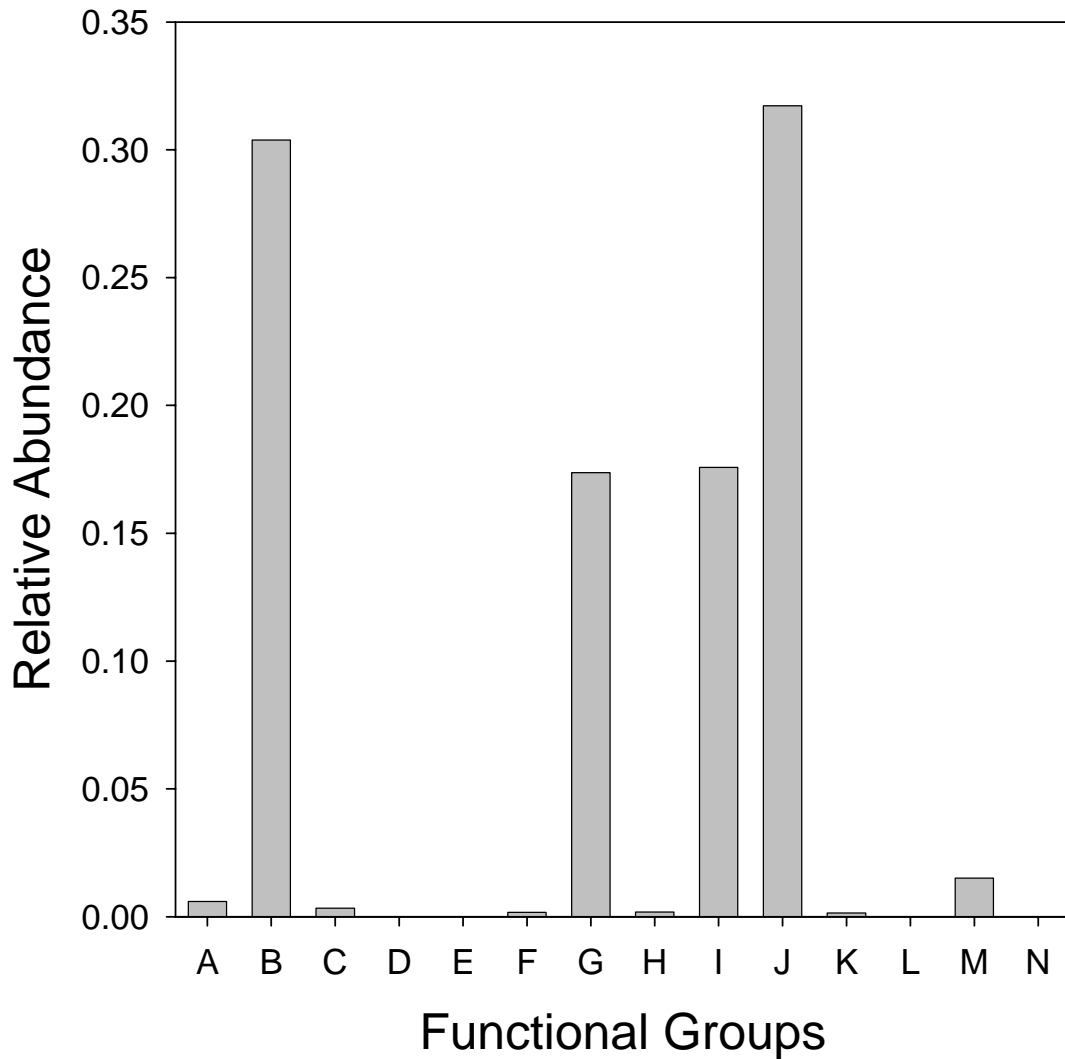


Figure B.39. Functional groupings of stream fish from Cottonwood Creek, Fisher County, in the Brazos River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

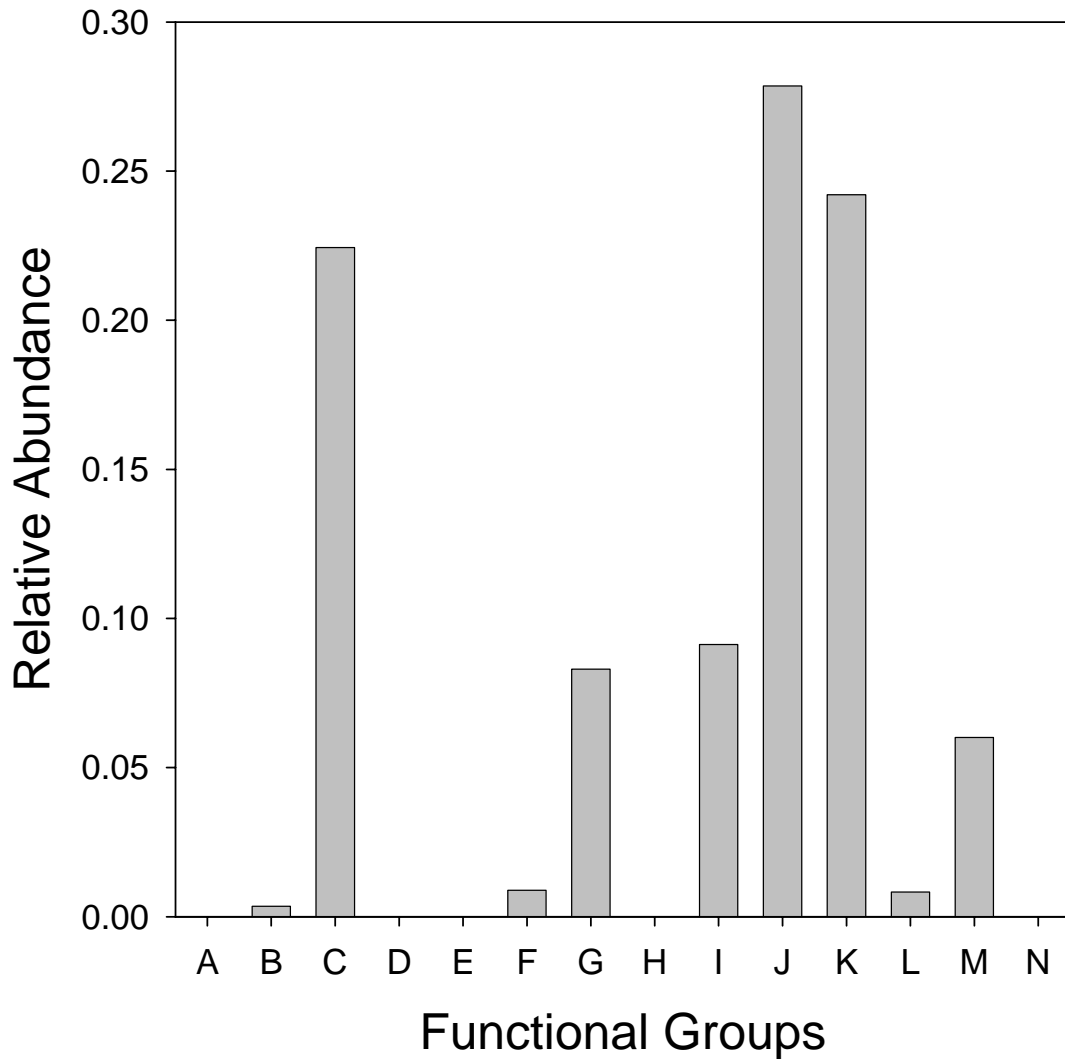


Figure B.40. Functional groupings of stream fish from Neils Creek, Bosque County, in the Brazos River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

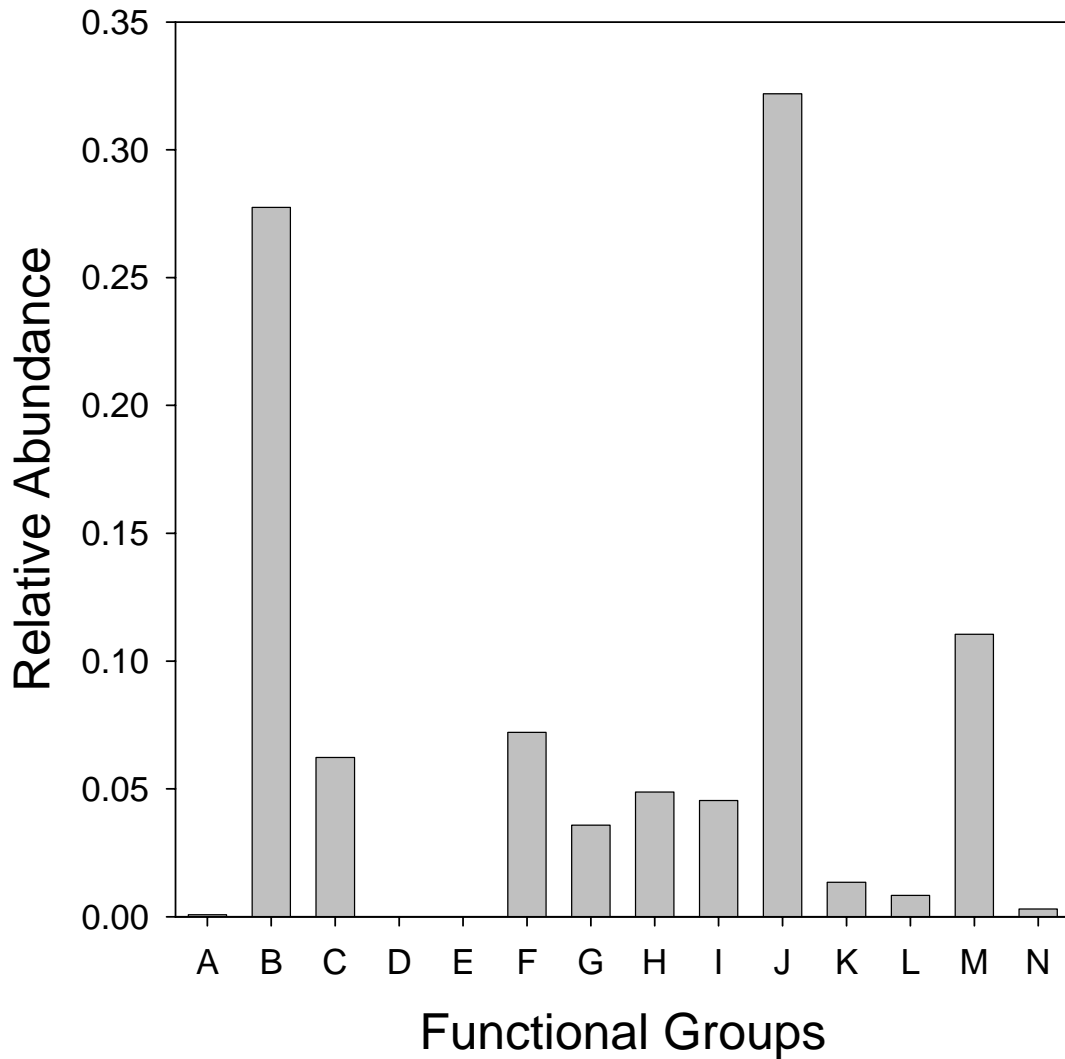


Figure B.41. Functional groupings of stream fish from Deer Creek, Falls County, in the Brazos River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

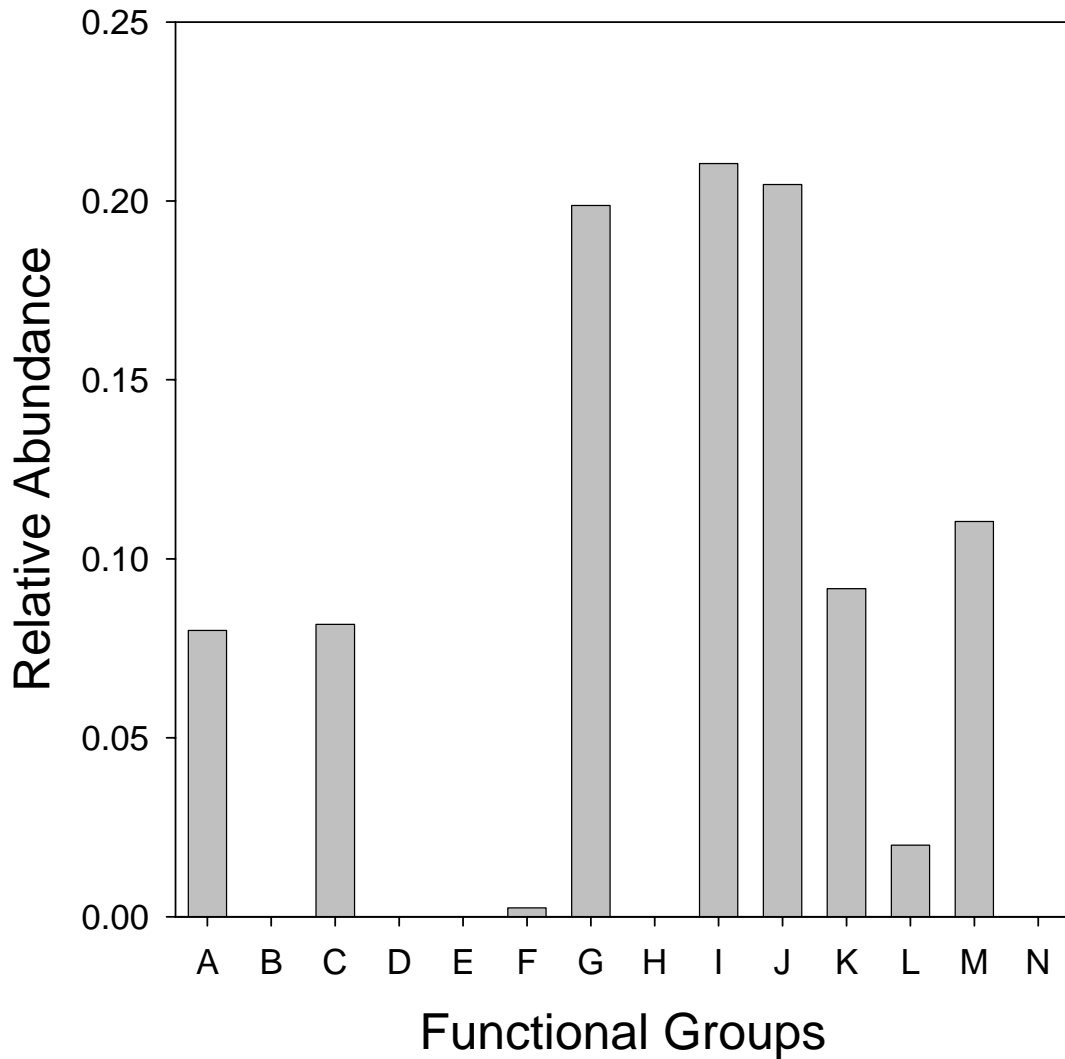


Figure B.42. Functional groupings of stream fish from West Rocky Creek, Irion County, in the Colorado River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

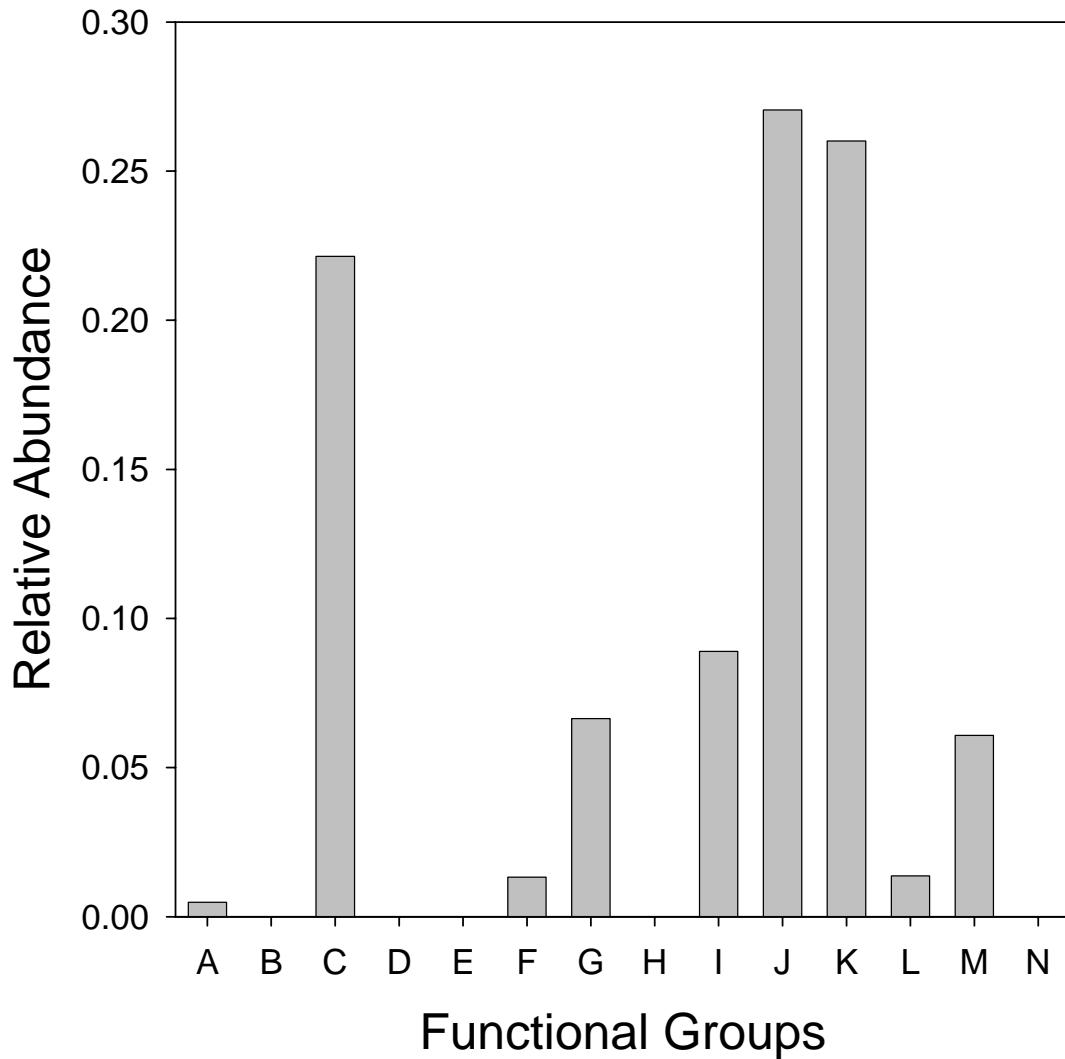


Figure B.43. Functional groupings of stream fish from Steele Creek, Bosque County, in the Brazos River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

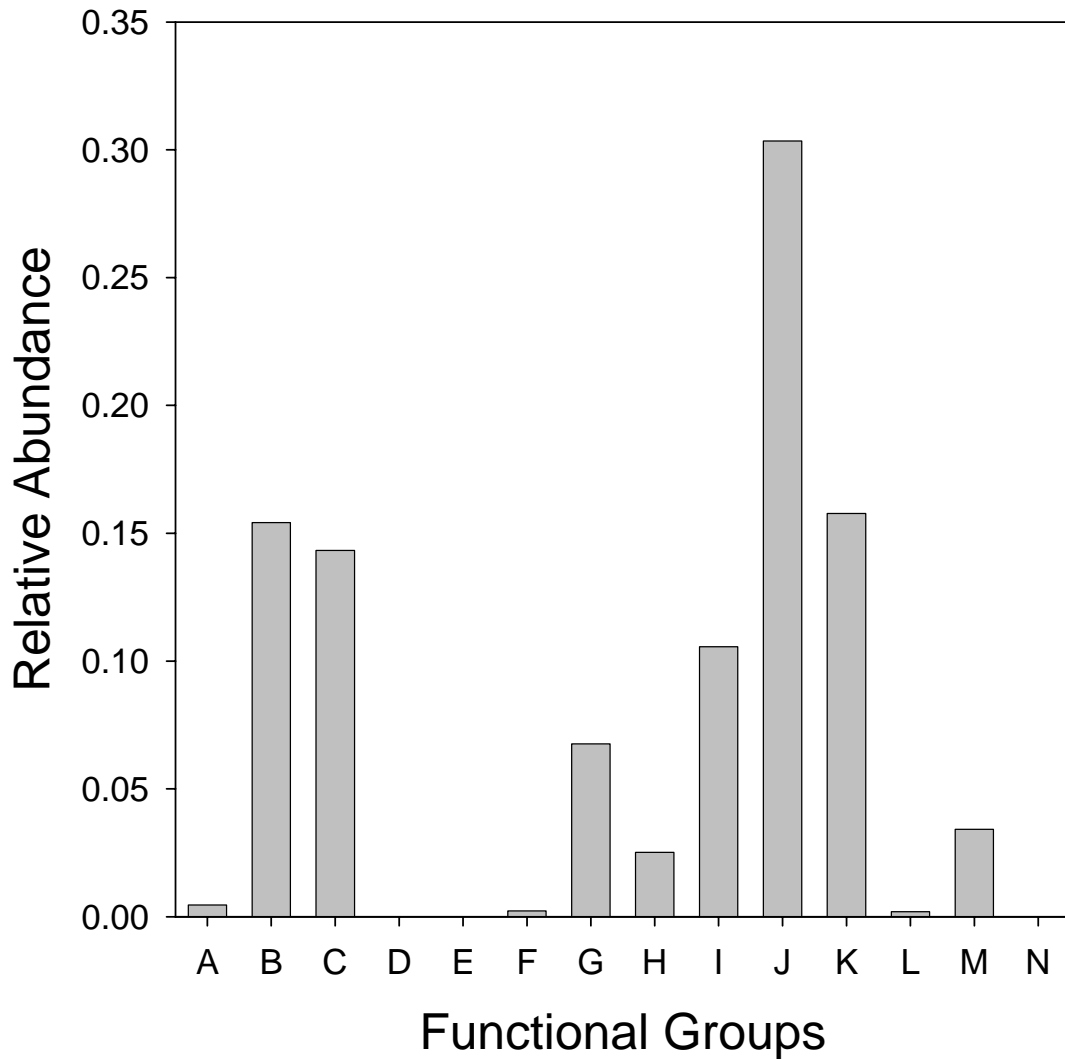


Figure B.44. Functional groupings of stream fish from Colony Creek, Eastland County, in the Brazos River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

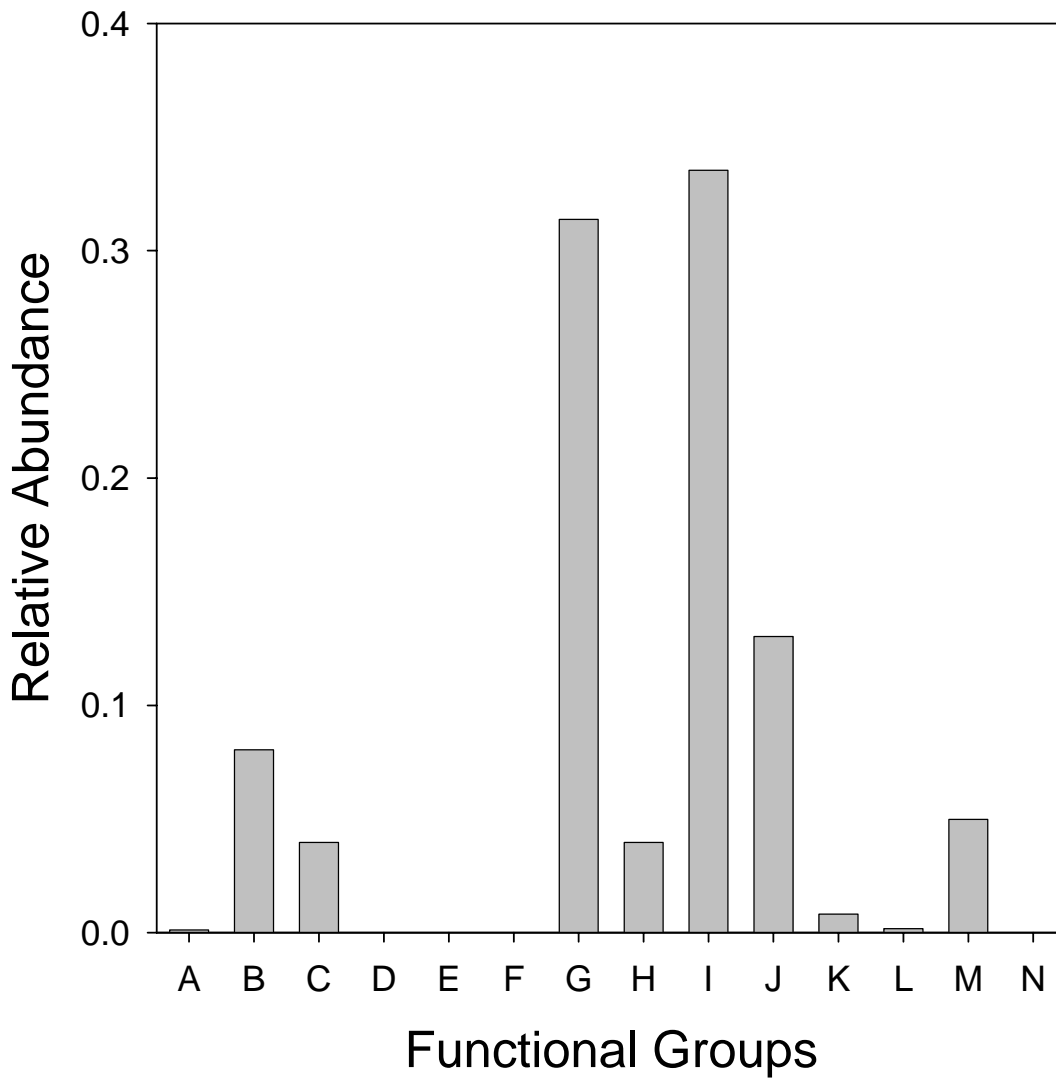


Figure B.45. Functional groupings of stream fish from Deadman Creek, Jones County, in the Brazos River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

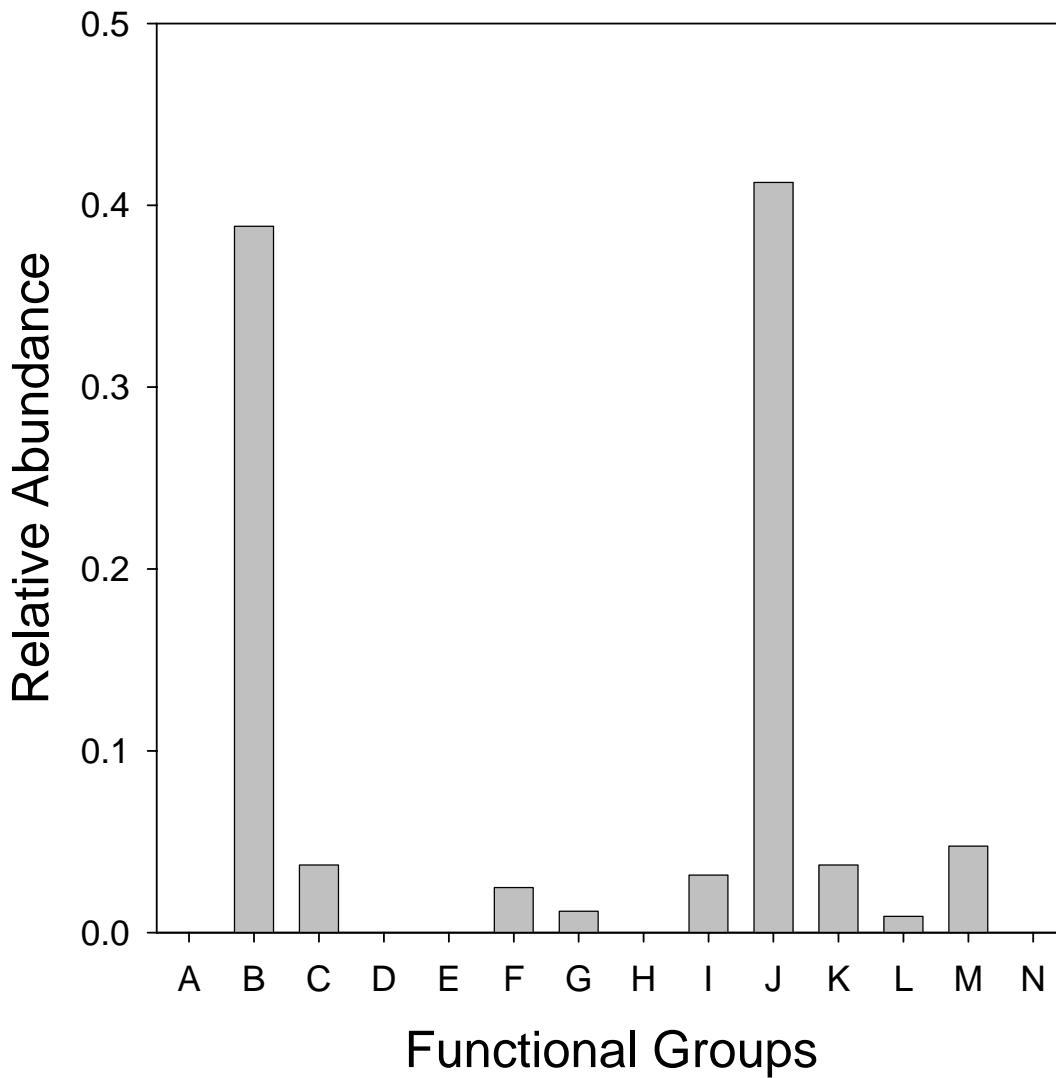


Figure B.46. Functional groupings of stream fish from Auds Creek, Lamar County, in the Sulphur River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

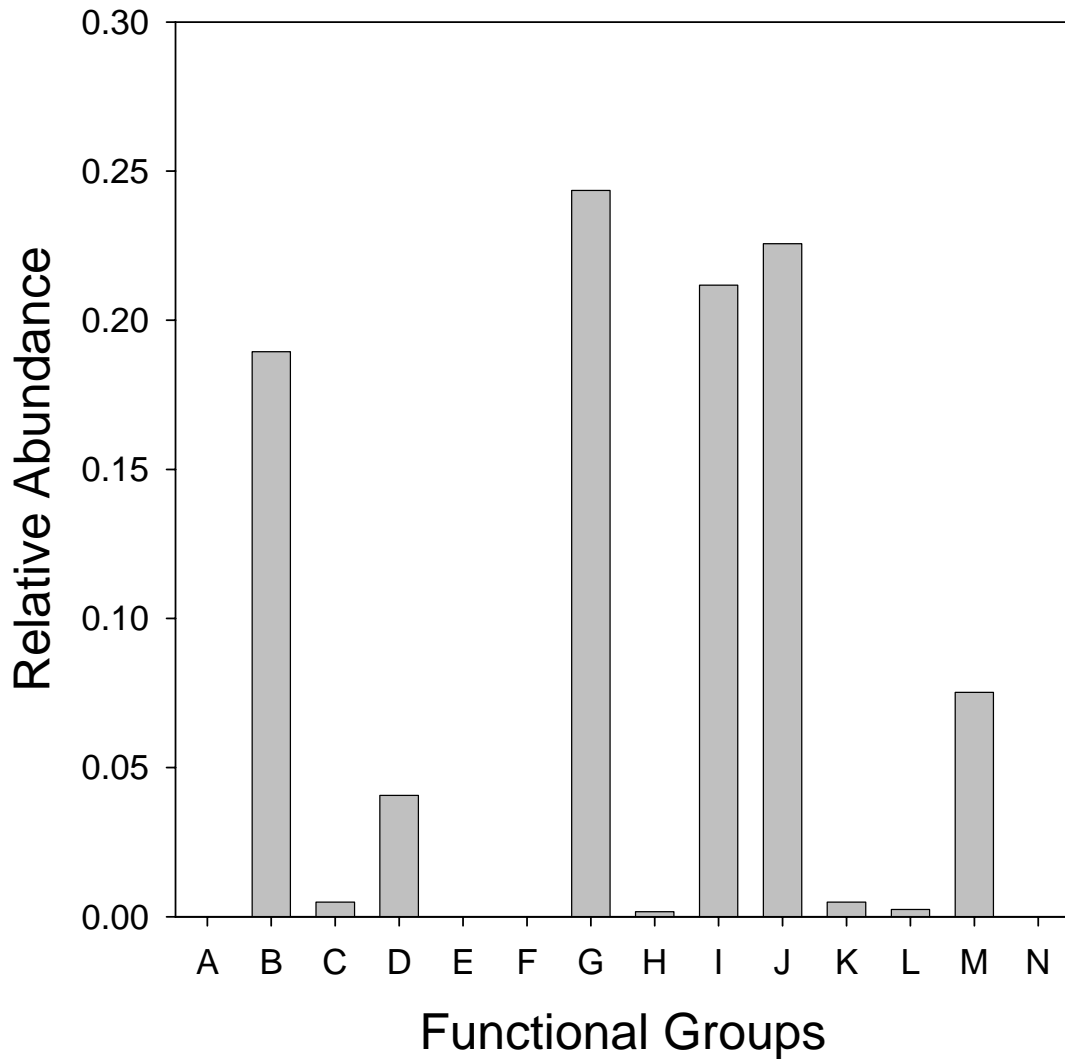


Figure B.47. Functional groupings of stream fish from Bluff Creek, Scurry County, in the Colorado River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

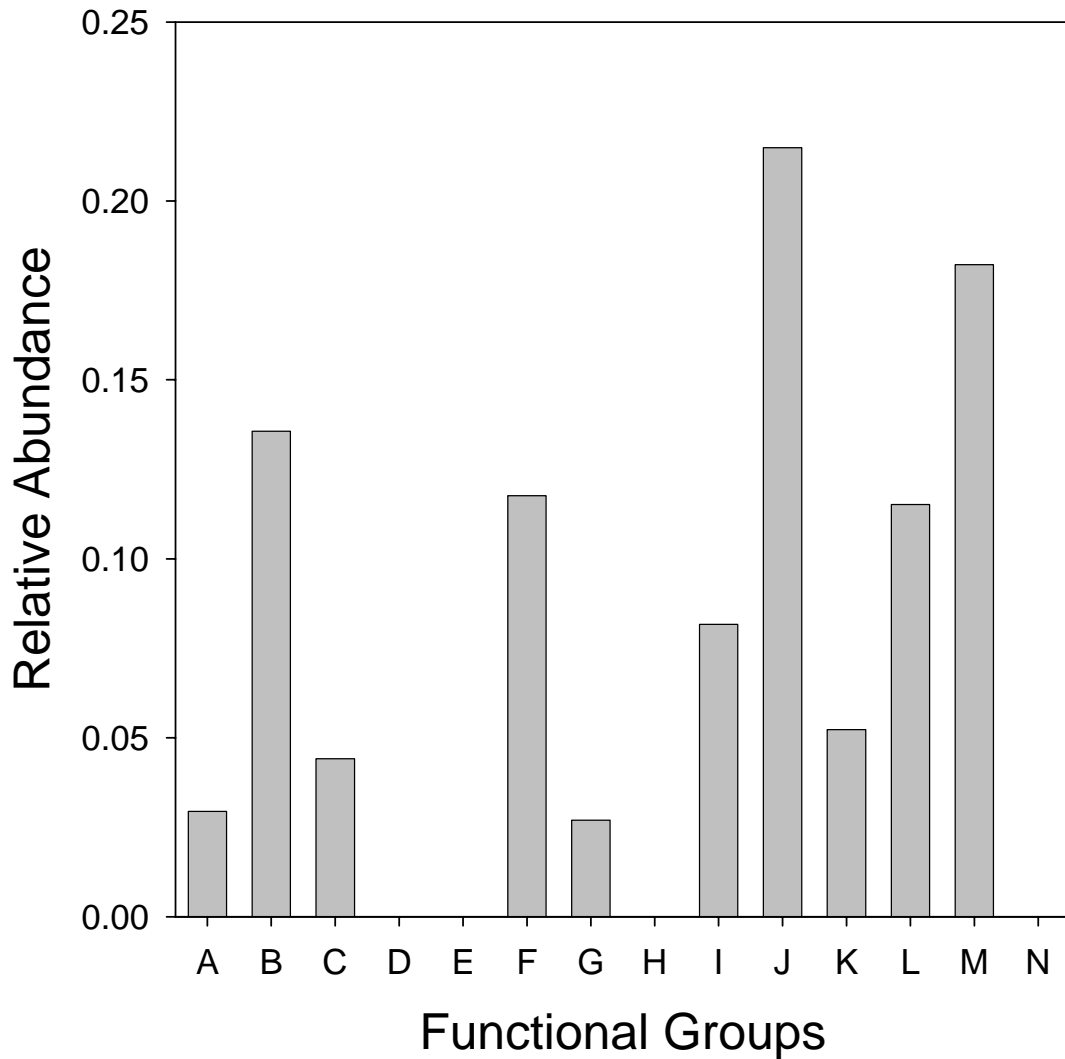


Figure B.48. Functional groupings of stream fish from Wilson Creek, Collin County, in the Trinity River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

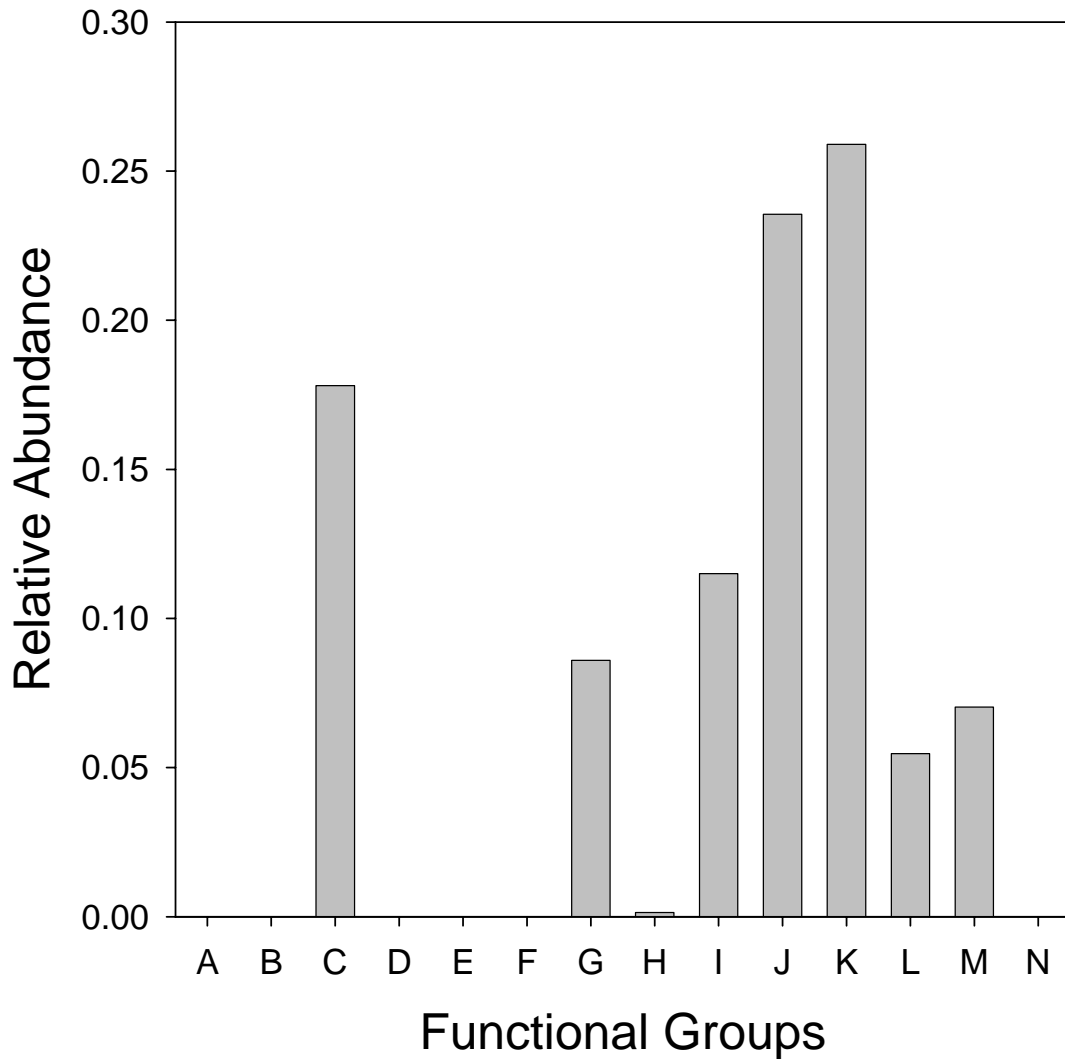


Figure B.49. Functional groupings of stream fish from Ioni Creek, Pal Pinto County, in the Brazos River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

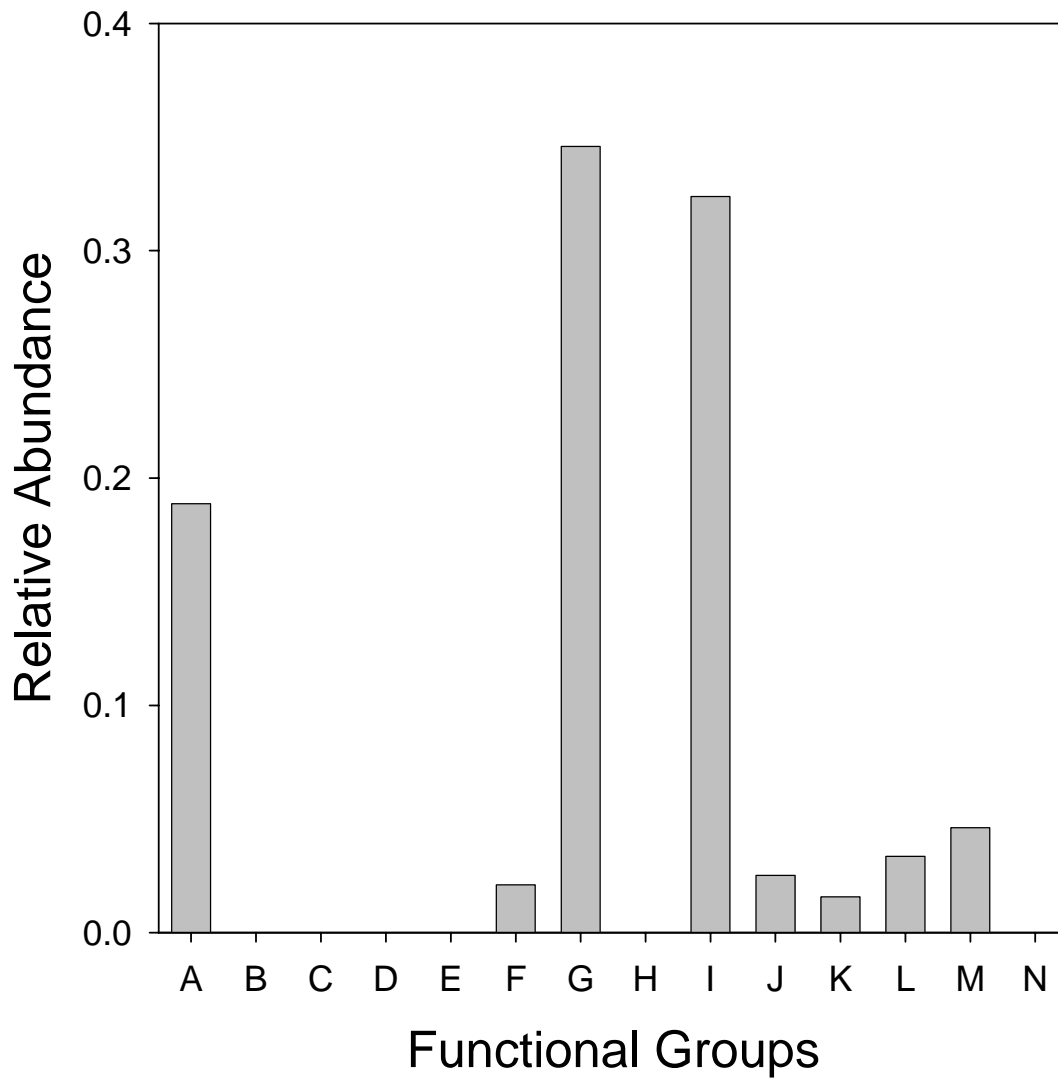


Figure B.50. Functional groupings of stream fish from Bluff Creek, McLennan County, in the Brazos River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

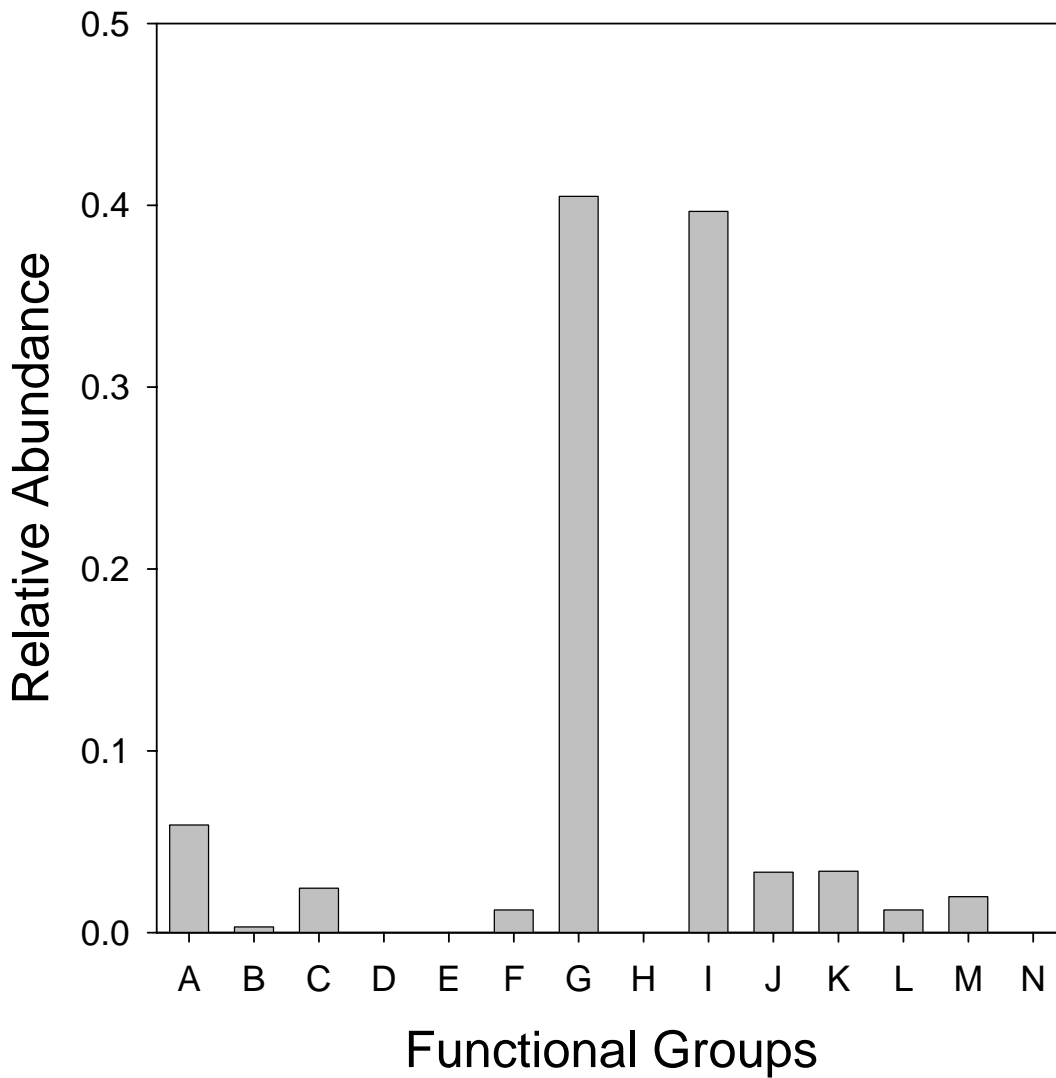


Figure B.51. Functional groupings of stream fish from Willis Creek, Williamson County, in the Brazos River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

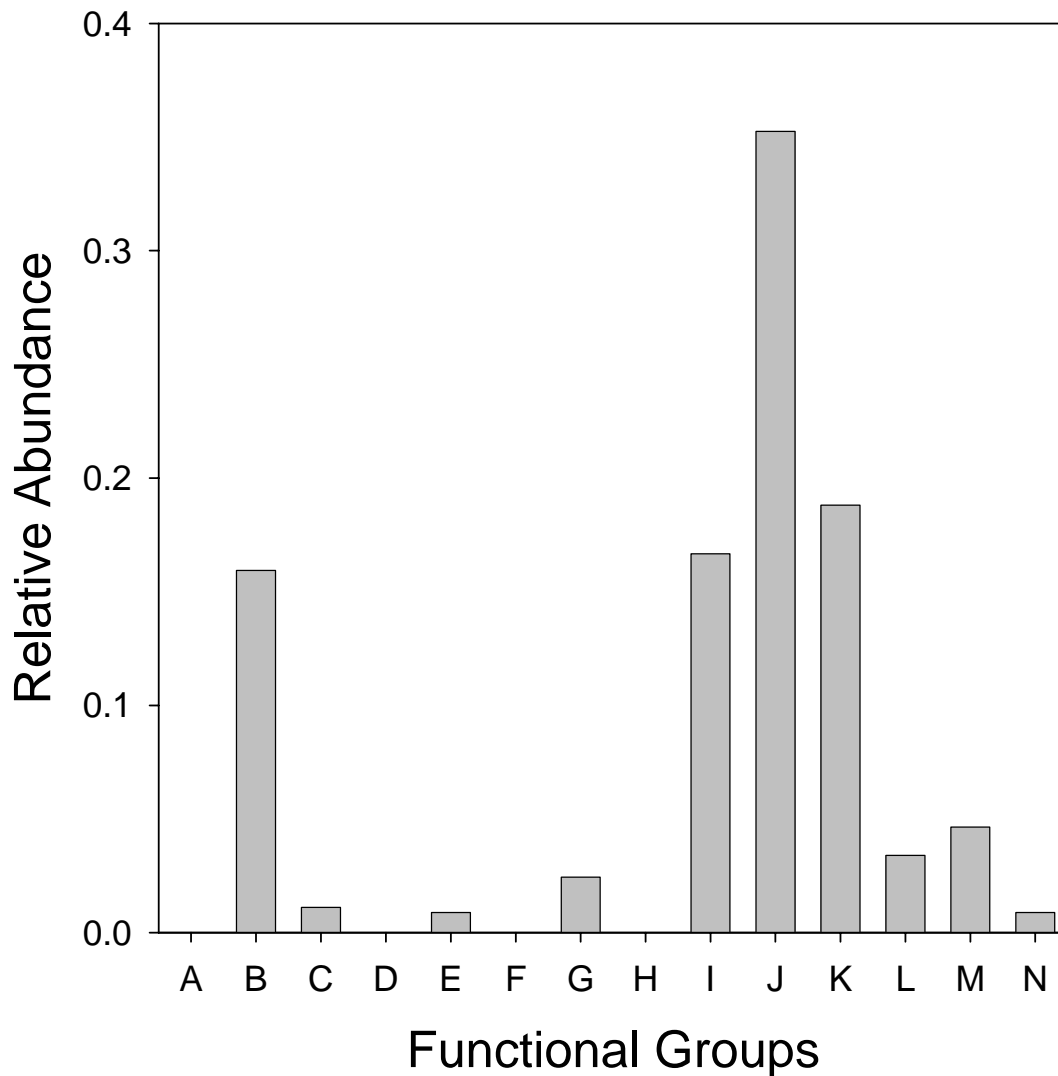


Figure B.52. Functional groupings of stream fish from Geronimo Creek, Guadalupe County, in the Guadalupe River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

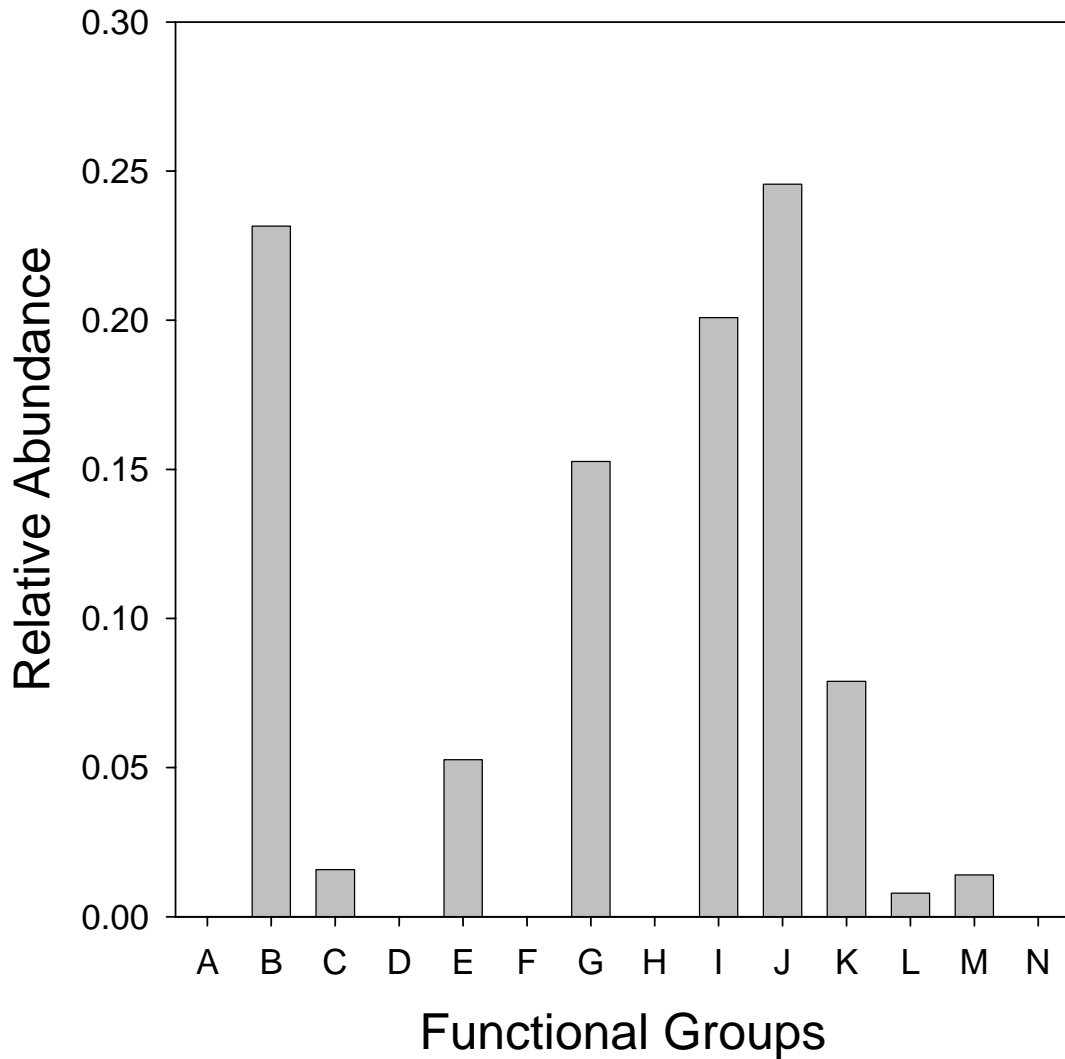


Figure B.53. Functional groupings of stream fish from Wolf Creek, Lipscomb County, in the Canadian River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

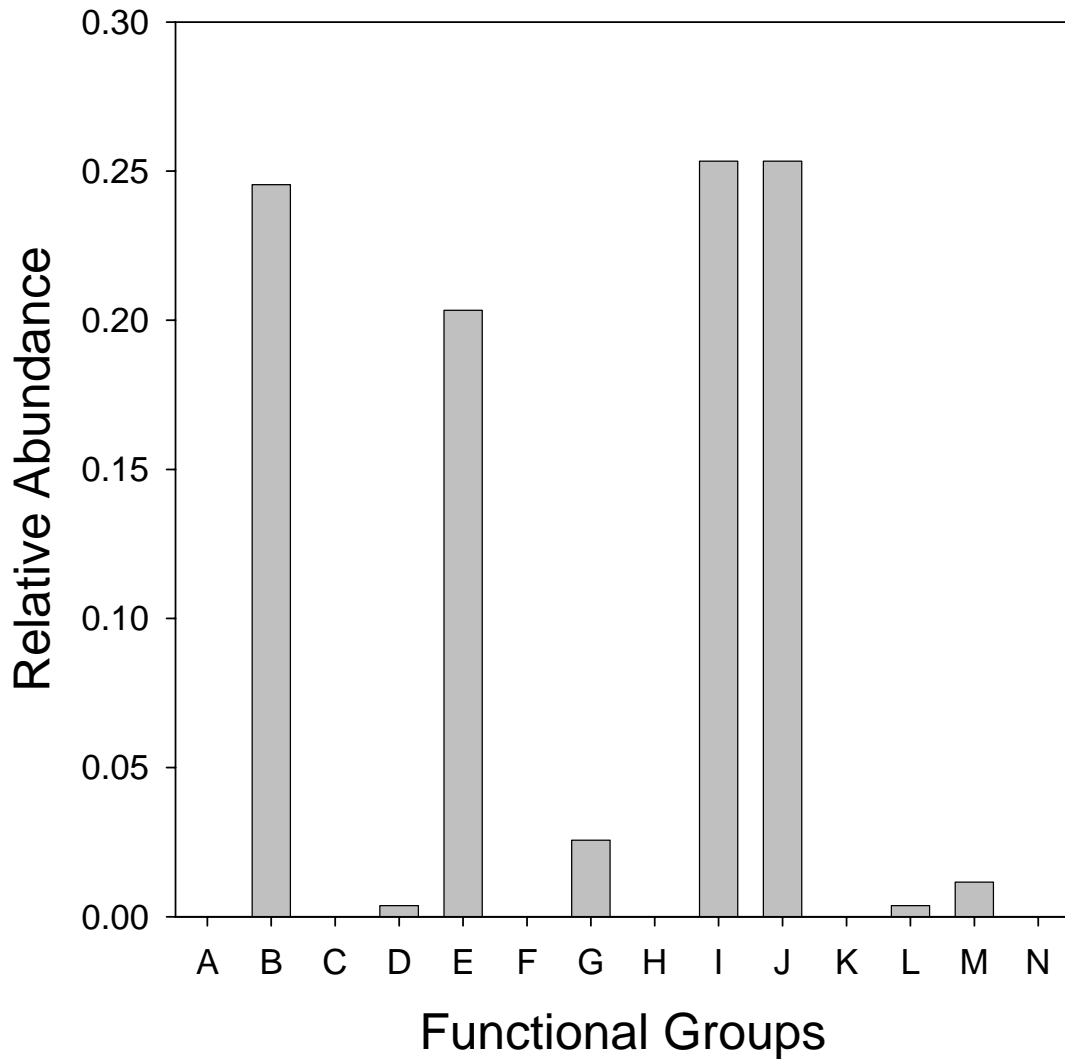


Figure B.54. Functional groupings of stream fish from McClellan Creek, Gray County, in the Red River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

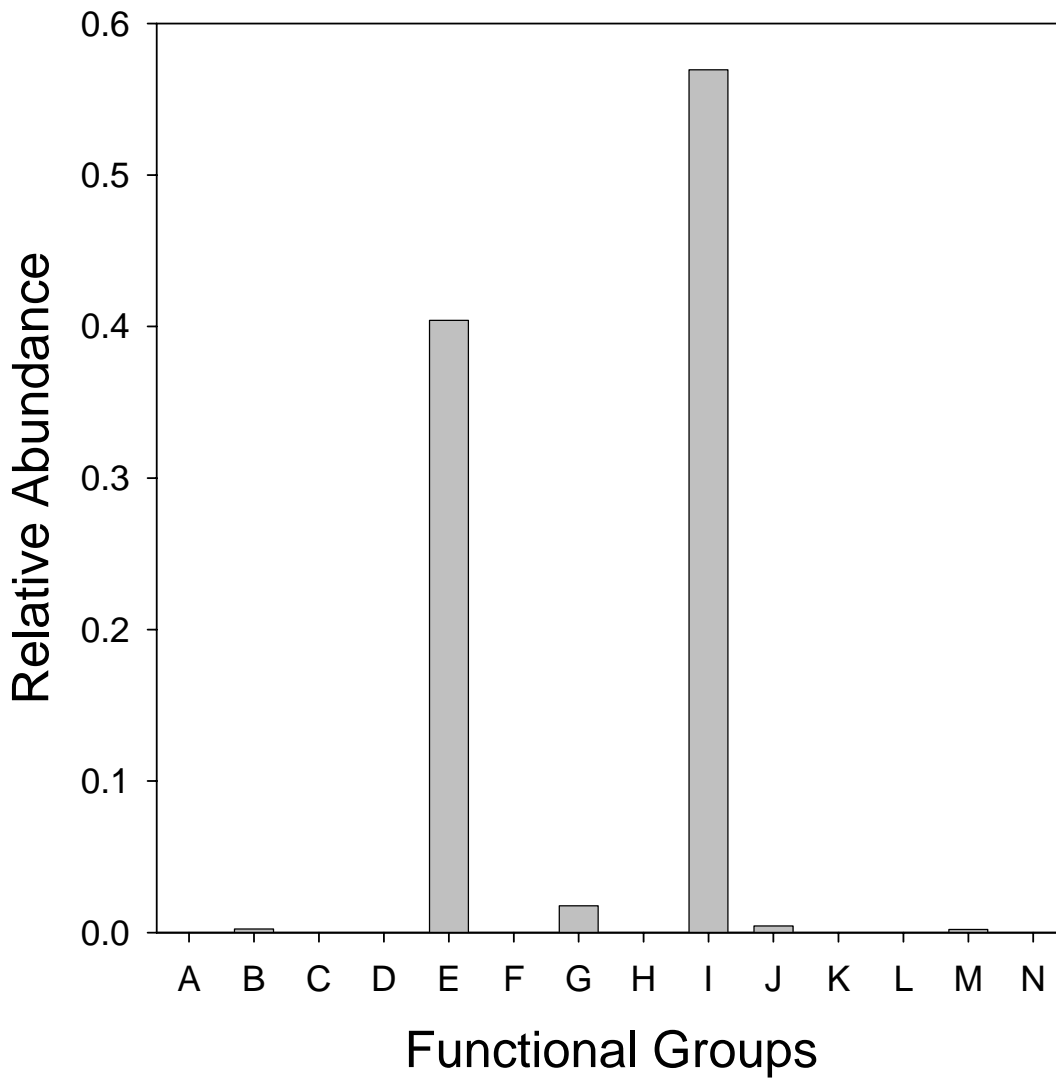


Figure B.55. Functional groupings of stream fish from Whitefish Creek, Donley County, in the Red River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

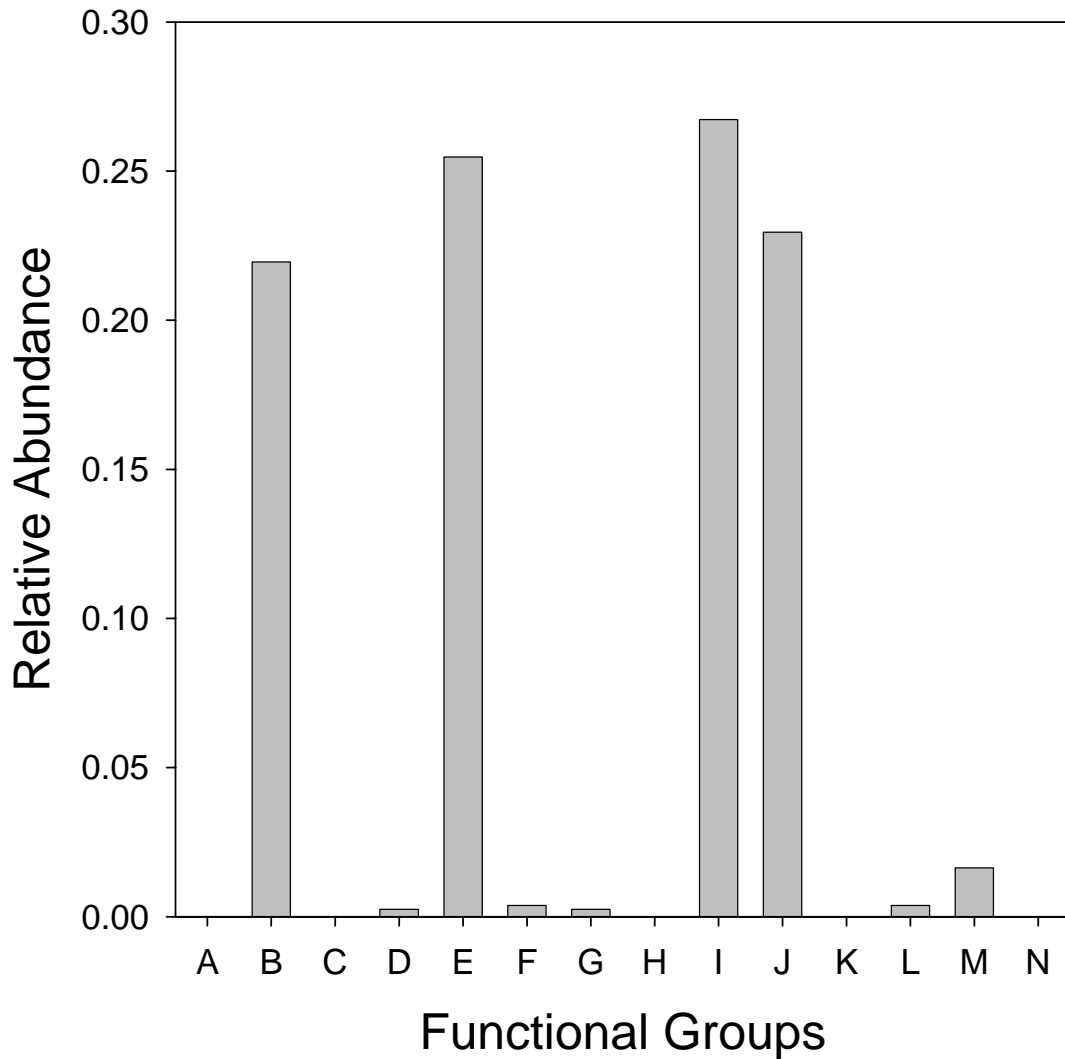


Figure B.56. Functional groupings of stream fish from Lelia Lake Creek, Donley County, in the Red River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

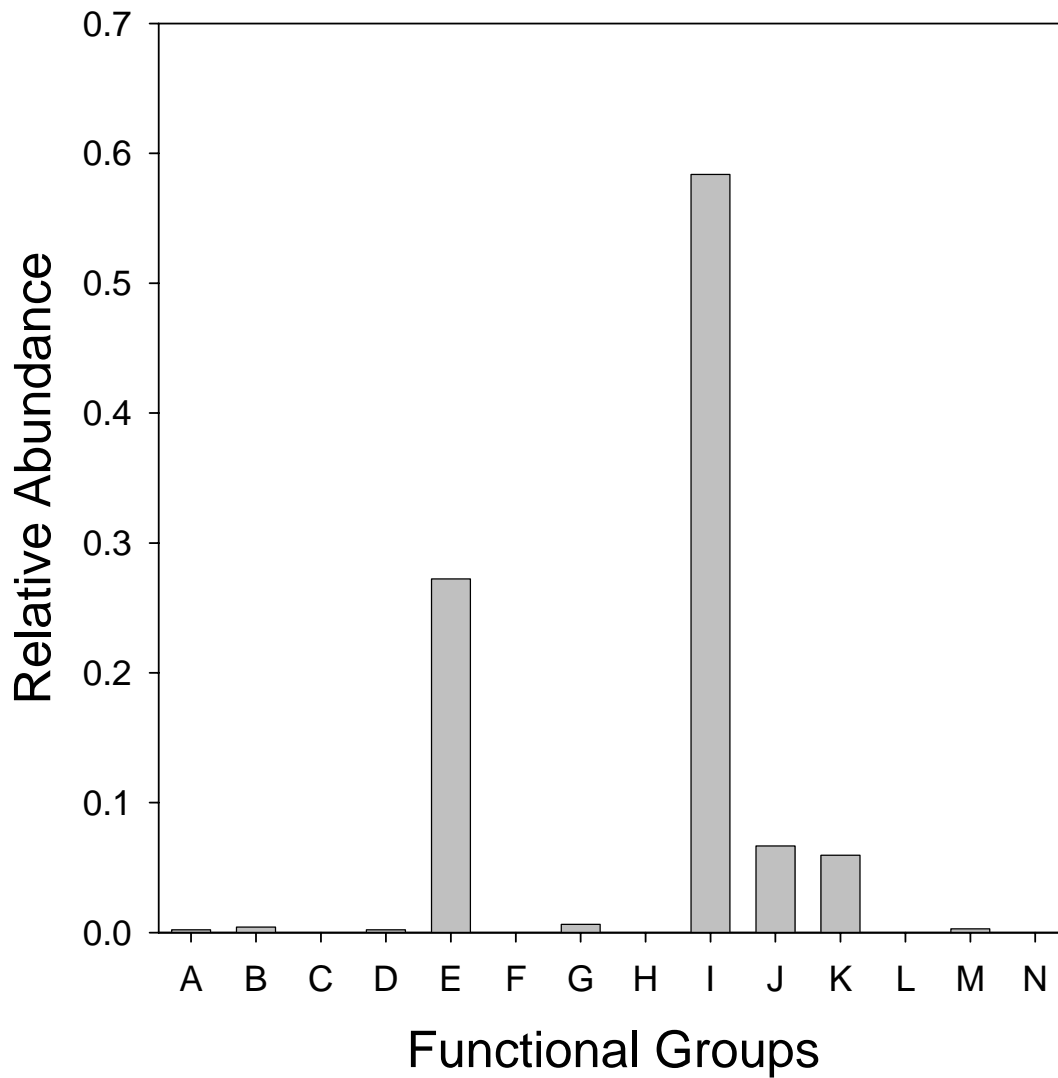


Figure B.57. Functional groupings of stream fish from Saddlers Creek, Donley County, in the Red River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

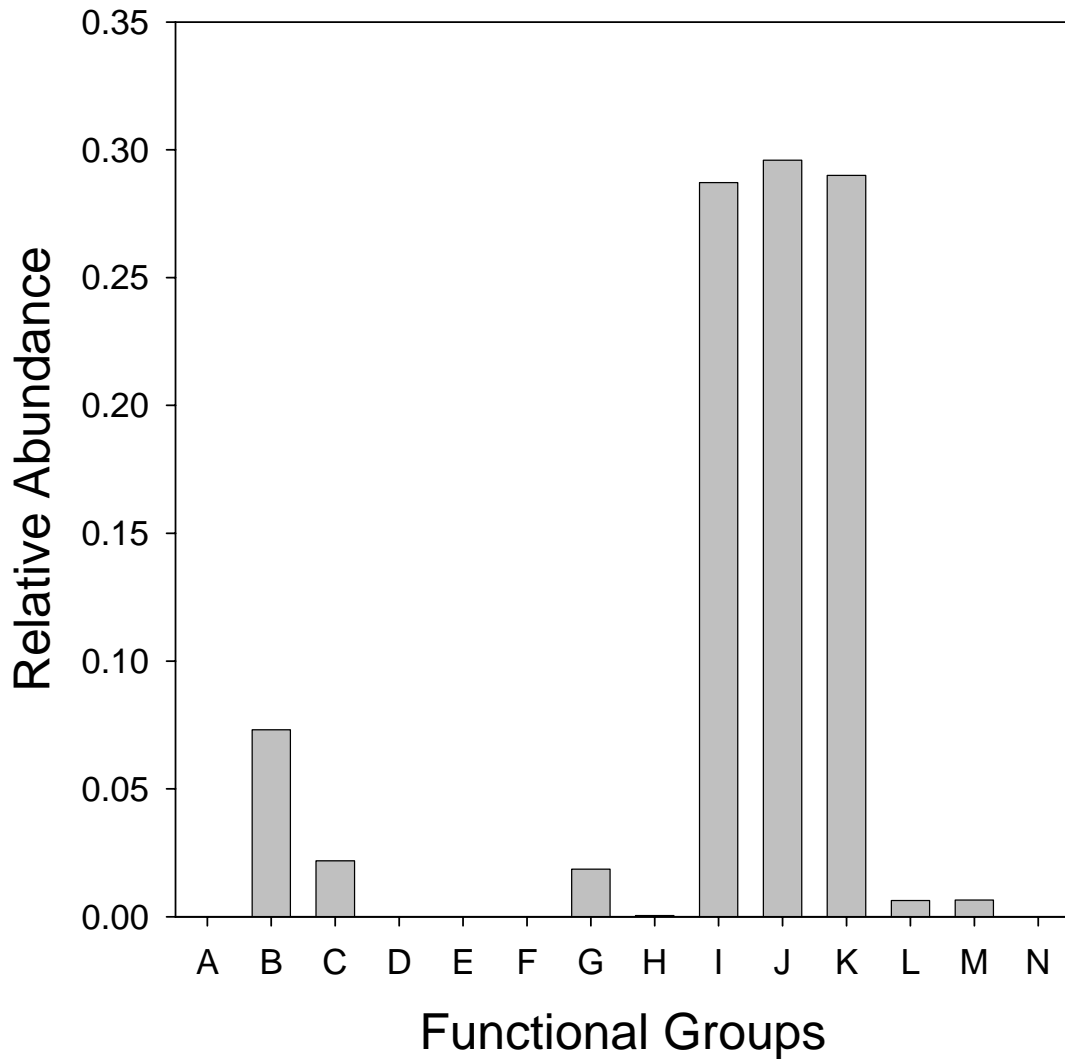


Figure B.58. Functional groupings of stream fish from Devils River, Val Verde County, in the Rio Grande River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

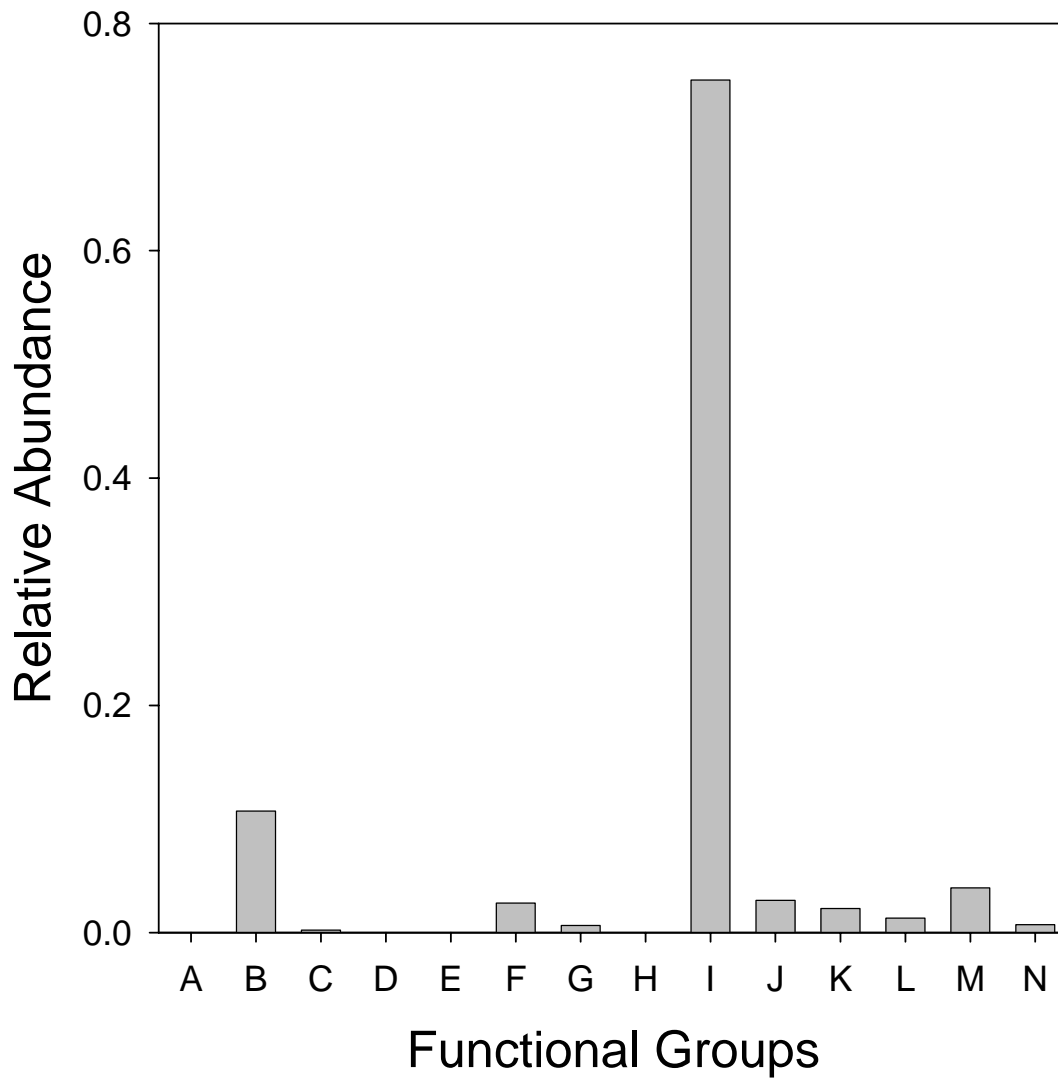


Figure B.59. Functional groupings of stream fish from Independence Creek, Terrell County, in the Rio Grande River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

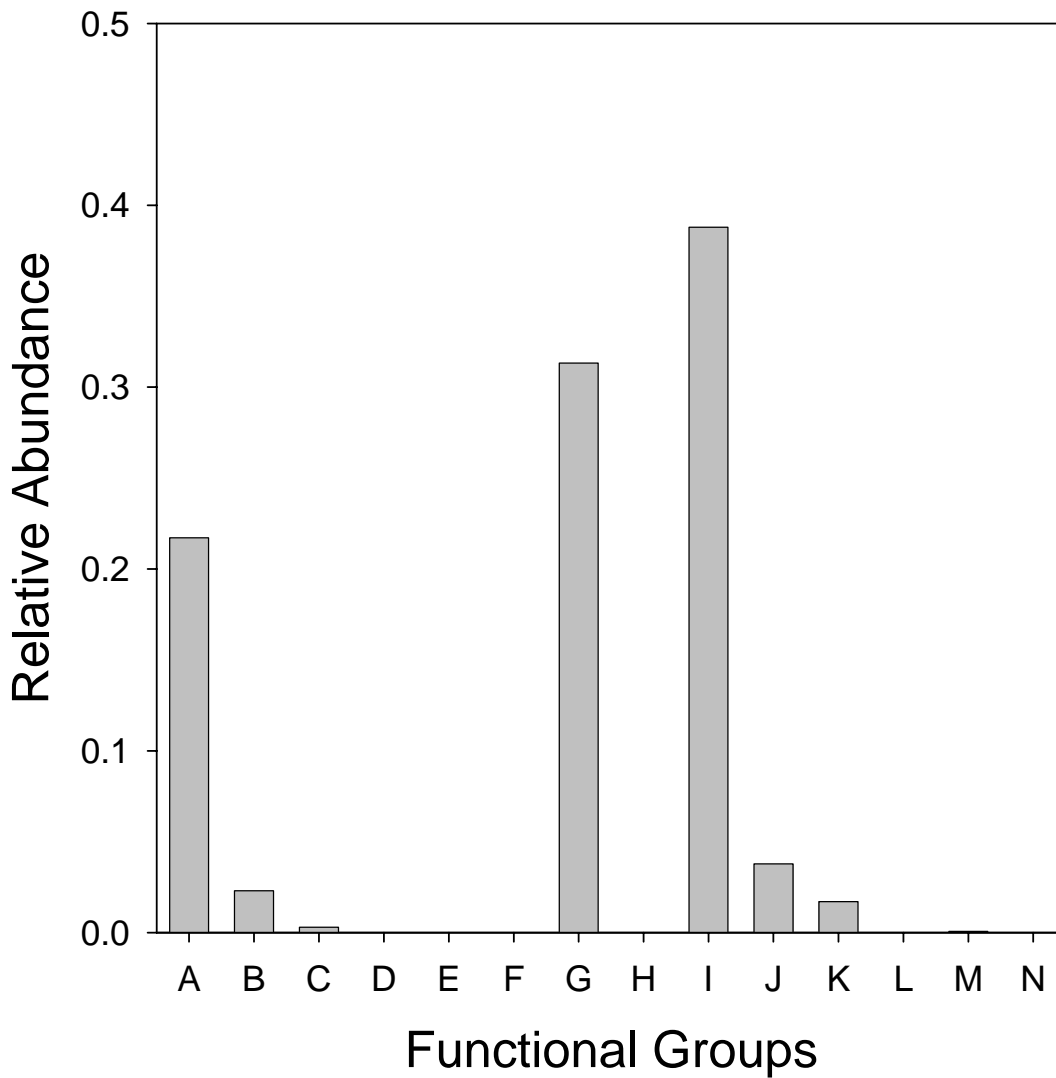


Figure B.60. Functional groupings of stream fish from Alamito Creek, Presidio County, in the Rio Grande River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

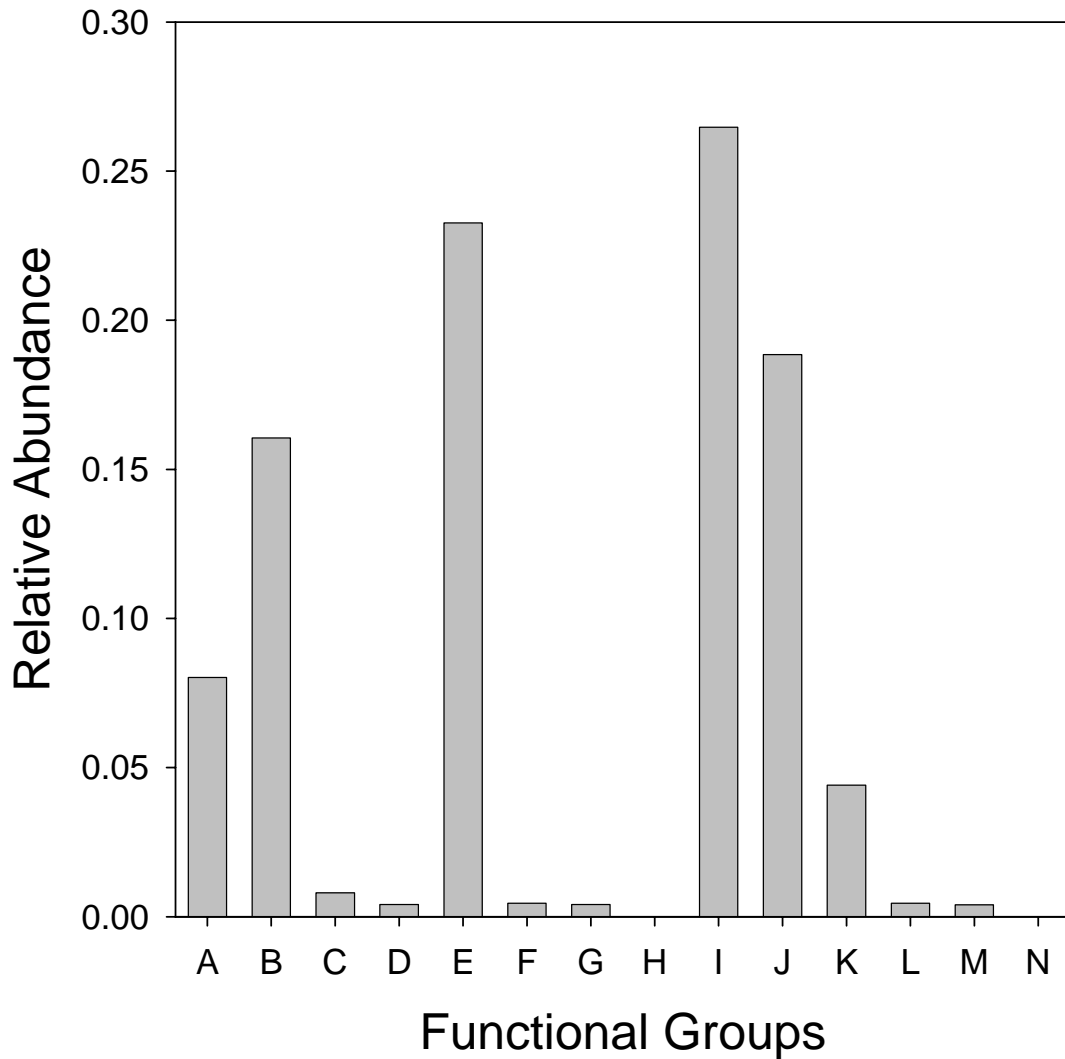


Figure B.61. Functional groupings of stream fish from Terlingua Creek, Brewster County, in the Rio Grande River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores.

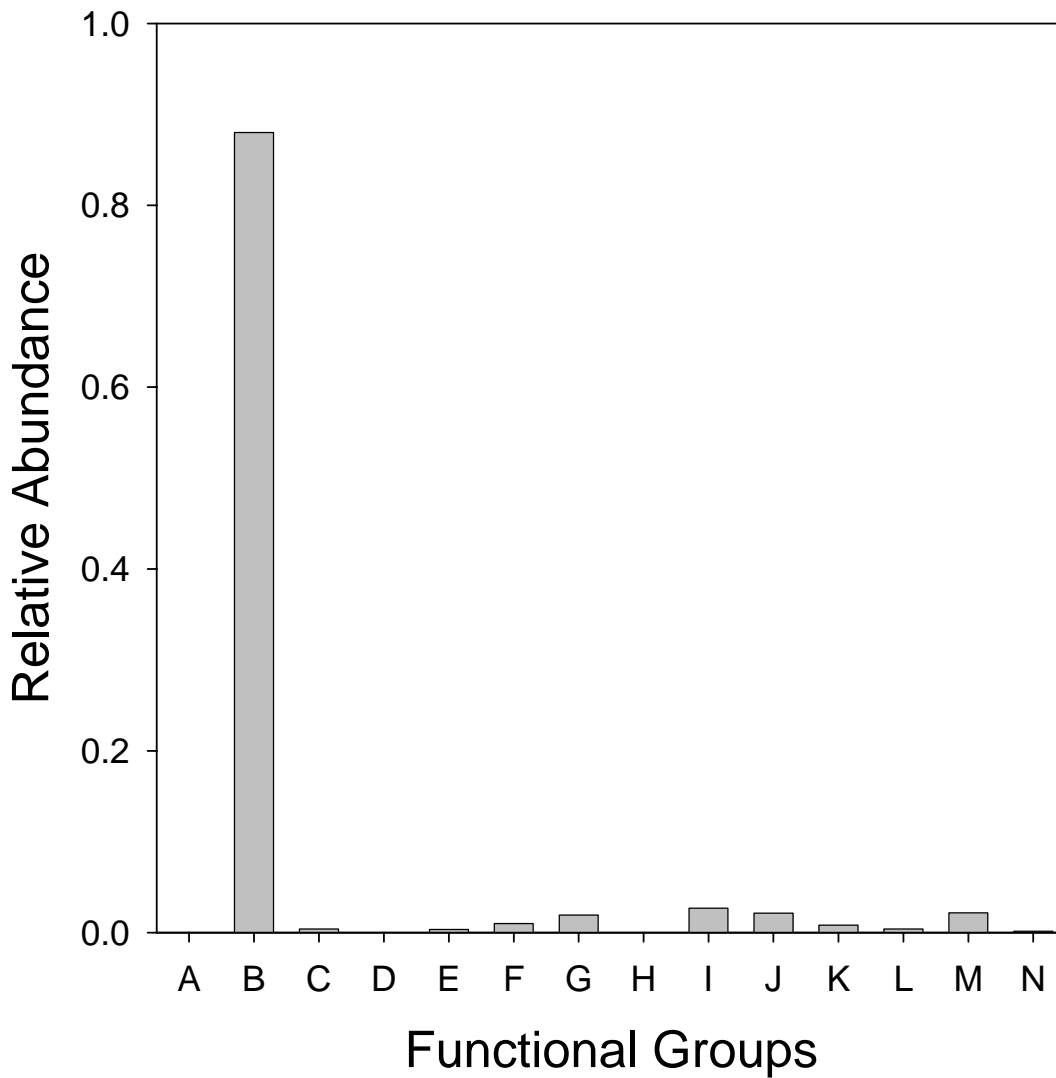


Figure B.62. Functional groupings of stream fish from Live Oak Creek, Crockett County, in the Rio Grande River basin: (A) grazers, (B) browsers, (C) benthic detritivores, (D) mud or sand eaters, (E) disturbance pickers, (F) scavengers, (G) egg eaters, (H) filter feeders, (I) surface feeders, (J) water-column particulate feeders, (K) benthic pickers, (L) snail crushers, (M) suction piscivores, and (N) biting piscivores

APPENDIX C

MATLAB FUNCTIONS FOR CALCULATING SPECIES ABUNDANCES BASED ON NICHE APPORTIONMENT MODELS

```
% BROKENSTICK: This function provides abundance data that follows MacArthur's Broken Stick Model
% according to simultaneous breakage, the formula provided in Magurran (1988), or Tokeshi's
% sequential breakage (1990).
%
% Usage: Abundance = brokenstick(S,N,model,rel)
%
% S = the total number of species for each community
% N = the total number of individuals in each community
% model = optional, specifies whether to use a simultaneous breakage (0), the deterministic equation
%       version (1) , or sequential breakage (2) {default = 1}
% rel = optional, specifies whether or not to make the abundances relative {default = 0}
% -----
% Abundance = a [1 x S] vector of species abundances
%
% Chris L. Higgins 3/5/2003
%
% Magurran, A.E. 1988. Ecological Diversity and Its Measurement. Princeton University
%   Press. Princeton, NJ. 179 pps.
%
% Tokeshi, M. 1990. Niche apportionment or random assortment: species abundance patters revisited.
%   Journal of Animal Ecology, 59: 1129-1146.
%
```

```
function Abundance = brokenstick(S,N,model,rel)

    if(nargin < 3)
        model = [];
    end;
    if(nargin < 4)
        rel = [];
    end;
    if isempty(model)
        model = 1;
    end;
    if isempty(rel)
        rel = 0;
    end;

    Abundance = zeros(1,S);

    if(model == 0)
        % Based on simultaneous breakage
        r = rand(1,S-1) * N;
        r = sort(r);
        x = [0 r N];
        for i = 1:S
            Abundance(i) = (x(i+1) - x(i));
        end;
    end;
end;
```



```

end;
Abundance = abs(sort(-Abundance));
end;

if(model == 1)                                % Based on Magurran
    for i = 1:S
        n = 0;
        for j = i:S
            n = n + (1 / j);
        end;
        Abundance(i) = (N/S) * sum(n);
    end;
end;

if(model == 2)                                % Based on sequential breakage (probability)
    x = [0 1];
    for i = 1:S-1
        in = rand;
        ind = find(x >= in);
        D = x(ind(1)) - x(ind(1)-1);
        r = rand * D;
        s = x(ind(1)-1) + r;
        x = [x s];
        x = sort(x);
    end;
    for j = 1:S
        Ab(j) = (x(j+1) - x(j)) * N;
    end;
    Abundance = abs(sort(-Ab));
end;

if(rel ~= 0)
    Abundance = Abundance / N;
end;

return;

```

```

% DOMINDECAY: This function provides the expected species abundances based on Tokeshi (1990)
% model of "Dominance Decay." In this model, "a new species always invades the niche space of the
% most abundant species of an existing assemblage."
%
% Usage: Abundance = domindecay(S,N,rel)
%
% S = the total number of species for each community
% N = the total number of individuals in each community
% rel = optional, specifies whether or not to make the abundances relative {default = 0}
% -----
% Abundance = a [S x 1] vector of expected species abundances
%
% Chris L. Higgins 3/5/2003
%
% Tokeshi, M. 1990. Niche apportionment or random assortment: species abundance patterns revisited.
% Journal of Animal Ecology, 59: 1129-1146.
%

```

```

function Abundance = domindecay(S,N,c,rel)

```

```

    if(nargin < 3)
        c = [];
    end;
    if(nargin < 4)
        rel = [];
    end;

    if isempty(c)
        c = 0;
    end;
    if isempty(rel)
        rel = 0;
    end;

    Abundance = zeros(1,S);
    available = N;

    x = [0 1];

    for i = 1:S
        for m = 2:length(x)
            Dist(m-1) = (x(m) - x(m-1));
        end;
        ind = find(Dist == max(Dist));
        rx = rand * max(Dist);
        s = x(ind) + rx;
        x = [x s];
        x = sort(x);
    end;

    for j = 1:S
        Ab(j) = (x(j+1) - x(j)) * N;
    end;

```

```
Abundance = abs(sort(-Ab));  
  
if(c == 1)  
    Abundance = ceil(Abundance);  
end;  
  
if(rel ~=0)  
    Abundance = Abundance / N;  
end;  
  
return;
```

```

% RANDASSORT: This function provides abundance data that follows the random assortment model of
% Tokeshi. "This model refers to a situation where abundances of different species are not mutually
% related at all. This would be conceived of either as a result of non-correspondences between niche
% apportionment and species abundance, or as a non-hierarchical, dynamic apportionment of niche
% under a highly variable environment."
%
% Usage: Abundance = randassort(S,N,rel)
%
% S = the total number of species for each community
% N = the total number of individuals in each community
% rel = optional, specifies whether or not to make the abundances relative {default = 0}
% -----
% Abundance = a [S x 1] vector of expected species abundances
%
% Chris L. Higgins 3/5/2003
%
% Tokeshi, M. 1990. Niche apportionment or random assortment: species abundance patterns revisited.
% Journal of Animal Ecology, 59: 1129-1146.
%

function Abundance = randassort(S,N,c,rel)

    if(nargin < 3)
        c = [];
    end;
    if(nargin < 4)
        rel = [];
    end;

    if isempty(c)
        c = 0;
    end;
    if isempty(rel)
        rel = 0;
    end;

    Abundance = zeros(1,S);

    for i = 1:S
        RelAbund = (0.5^i)/(1-(0.5^S));
        Abundance(i) = RelAbund * N;
    end;

    if(c == 1)
        Abundance = ceil(Abundance);
    end;

    if(rel ~=0)
        Abundance = Abundance / N;
    end;

return;

```

```

% PREEMPTION: This function provides the expected species abundances based on Tokeshi (1990) model
% of "Dominance Preemption." In this model, "the first species exerts its dominance by preempting
% more than half the total niche available and leaves the remainder to be exploited by the second
% species in the same manner, and so on."
%
% Usage: Abundance = preemption(S,N,rel)
%
% S = the total number of species for each community
% N = the total number of individuals in each community
% rel = optional, specifies whether or not to make the abundances relative {default = 0}
% -----
% Abundance = a [S x 1] vector of expected species abundances
%
% Chris L. Higgins 3/5/2003
%
% Tokeshi, M. 1990. Niche apportionment or random assortment: species abundance patterns revisited.
% Journal of Animal Ecology, 59: 1129-1146.
%

```

```

function Abundance = preemption(S,N,c,rel)

```

```

    if(nargin < 3)
        c = [];
    end;
    if(nargin < 4)
        rel = [];
    end;

    if isempty(c)
        c = 0;
    end;
    if isempty(rel)
        rel = 0;
    end;

    Abundance = zeros(1,S);
    available = N;

    for i = 1:S
        stop = 0;
        while(stop == 0)
            r = rand;
            if(r >= 0.5)
                stop = 1;
            end;
        end;
        consumed = r * available;
        available = available - consumed;
        Abundance(i) = consumed;
    end;

    if(c == 1)
        Abundance = ceil(Abundance);
    end;

```

```
end;  
  
if(rel ~=0)  
    Abundance = Abundance / N;  
end;  
  
return;
```

```

% RANDFRACT: This function provides abundance data that follows the random fraction model of
% Tokeshi. In this model, "the niche is first divided at random (uniform) into two fractions, one of them
% is then randomly chosen and divided at random (uniform) into further two fractions, thus resulting
% in three fractions,... and so on."
%
% Usage: Abundance = randfract(S,N,rel)
%
% S = the total number of species for each community
% N = the total number of individuals in each community
% rel = optional, specifies whether or not to make the abundances relative {default = 0}
% -----
% Abundance = a [S x 1] vector of expected species abundances
%
% Chris L. Higgins 3/5/2003
%
% Tokeshi, M. 1990. Niche apportionment or random assortment: species abundance patterns revisited.
% Journal of Animal Ecology, 59: 1129-1146.
%

```

```

function Abundance = randfract(S,N,rel)

```

```

    if(nargin < 3)
        rel = [];
    end;
    if isempty(rel)
        rel = 0;
    end;

    Abundance = zeros(1,S);

    x = [0 1];

    for i = 1:S-1
        in = randperm(i);
        ind = in(1);
        D = x(ind+1) - x(ind);
        r = rand * D;
        s = x(ind) + r;
        x = [x s];
        x = sort(x);
    end;

    for j = 1:S
        Ab(j) = (x(j+1) - x(j)) * N;
    end;

    Abundance = abs(sort(-Ab));

    if(rel ~=0)
        Abundance = Abundance / N;
    end;

```

```

return;

```

```

% ASSEMBLAGE: This function produces 95% confidence intervals for degree of fit between
% various niche-based abundance models and empirical species abundance distributions.
%
% Usage: [Diff,DiffCI] = assemblage1(data,iter,dev,plot)
%
% data = a [r x c] matrix of species abundances for "r" different sites
% iter = optional, specifies the number of iterations to use when estimating the confidence intervals
%   {default = 1000}
% dev = optional, specifies which type of deviations to use when assessing the degree of fit
%   Sum-of-absolute-difference = 0
%   Sum-of-squared-differences = 1 {default}
%   Sum-of-chi-squared0difference = 2
% doplot = optional, specifies whether or not to plot the expected abundance {default = 0}
% -----
% Diff = a [r x 5] matrix of relative difference in degree of fit between model and data
% DiffCI = a [r x 2] matrix of corresponding confidence intervals
%
% Chris L. Higgins 5/5/2004
%

```

```

function [Diff,DiffCI] = assemblage(data,iter,dev,doplot)

    if(nargin < 2)                                % Allocate input arguments
        iter = [];
    end;
    if(nargin < 3)
        dev = [];
    end;
    if(nargin < 4)
        doplot = [];
    end;

    if isempty(iter)
        iter = 1000;
    end;
    if isempty(dev)
        dev = 1;
    end;
    if isempty(doplot)
        doplot = 0;
    end;

    [r,c] = size(data);                          % Determine the total number of sites and species

    Diff = [];
    for i = 1:r
        ind = find(data(i,:) > 0);                % Find the species that are present at each site
        Obs = data(i,ind);                        % Create a new vector of observed counts
        Obs = abs(sort(-Obs));                    % Rank the species abundances from high to low
        S = length(ind);                         % Calculate the species richness for each site
        N = sum(Obs);                             % Calculate the total # of individuals for each site
        SAD1 = zeros(iter,S);
        SAD2 = zeros(iter,S);
    end;

```



```

SAD3 = zeros(iter,S);
SAD4 = zeros(iter,S);
SAD5 = zeros(iter,S);
for j = 1:iter
    SAD1(j,:) = dominidecay(S,N); % Model the site according to dominance decay
    SAD2(j,:) = brokenstick(S,N,2); % Model the site according to brokenstick
    SAD3(j,:) = randfract(S,N); % Model the site according to random fraction
    SAD4(j,:) = randassort(S,N); % Model the site according to random assortment
    SAD5(j,:) = preemption(S,N); % Model the site according to dominance preemption
end;
Exp1 = mean(SAD1);
Exp2 = mean(SAD2);
Exp3 = mean(SAD3);
Exp4 = mean(SAD4);
Exp5 = mean(SAD5);
if(dev == 0)
    D1(i) = absdev(Obs,Exp1); % Calculate the sum-of-absolute-differences b/w Obs & Exp
    D2(i) = absdev(Obs,Exp2);
    D3(i) = absdev(Obs,Exp3);
    D4(i) = absdev(Obs,Exp4);
    D5(i) = absdev(Obs,Exp5);
end;
if(dev == 1)
    D1(i) = sumsqdev(Obs,Exp1); % Calculate the sum-of-squared-differences b/w Obs & Exp
    D2(i) = sumsqdev(Obs,Exp2);
    D3(i) = sumsqdev(Obs,Exp3);
    D4(i) = sumsqdev(Obs,Exp4);
    D5(i) = sumsqdev(Obs,Exp5);
end;
if(dev == 2)
    D1(i) = chi2(Obs,Exp1); % Calculate the chi-squared-differences b/w Obs & Exp
    D2(i) = chi2(Obs,Exp2);
    D3(i) = chi2(Obs,Exp3);
    D4(i) = chi2(Obs,Exp4);
    D5(i) = chi2(Obs,Exp5);
end;
D = [D1(i) D2(i) D3(i) D4(i) D5(i)];
D = D/sum(D);
Diff = [Diff;D];
end;

DiffCI = [];
for i = 1:r
    for k = 1:iter
        ind = find(data(i,:) > 0); % Find the species that are present at each site
        Z = data(i,ind);
        Z1 = makegrps([1:length(Z)],Z)';
        Xsamp = samplewr(Z1); % Create a bootstrapped vector of observed counts
        [u,f] = unique1(Xsamp);
        Obs = abs(sort(-f)); % Rank the species abundances from high to low
        S = length(ind); % Calculate the species richness for each site
        N = sum(Obs); % Calculate the total # of individuals for each site
        SAD1 = zeros(iter,S);
    end;
end;

```

```

SAD2 = zeros(iter,S);
SAD3 = zeros(iter,S);
SAD4 = zeros(iter,S);
SAD5 = zeros(iter,S);
for j = 1:iter
    SAD1(j,:) = dominidecay(S,N); % Model the site according to dominance decay
    SAD2(j,:) = brokenstick(S,N,2); % Model the site according to brokenstick
    SAD3(j,:) = randfract(S,N); % Model the site according to random fraction
    SAD4(j,:) = randassort(S,N); % Model the site according to random assortment
    SAD5(j,:) = preemption(S,N); % Model the site according to dominance preemption
end;
Exp1 = mean(SAD1);
Exp2 = mean(SAD2);
Exp3 = mean(SAD3);
Exp4 = mean(SAD4);
Exp5 = mean(SAD5);
if(dev == 0)
    D1(i) = absdev(Obs,Exp1); % Calculate the sum-of-absolute-differences b/w Obs & Exp
    D2(i) = absdev(Obs,Exp2);
    D3(i) = absdev(Obs,Exp3);
    D4(i) = absdev(Obs,Exp4);
    D5(i) = absdev(Obs,Exp5);
end;
if(dev == 1)
    D1(i) = sumsqdev(Obs,Exp1); % Calculate the sum-of-squared-differences b/w Obs & Exp
    D2(i) = sumsqdev(Obs,Exp2);
    D3(i) = sumsqdev(Obs,Exp3);
    D4(i) = sumsqdev(Obs,Exp4);
    D5(i) = sumsqdev(Obs,Exp5);
end;
if(dev == 2)
    D1(i) = chi2(Obs,Exp1); % Calculate the chi-squared-differences b/w Obs & Exp
    D2(i) = chi2(Obs,Exp2);
    D3(i) = chi2(Obs,Exp3);
    D4(i) = chi2(Obs,Exp4);
    D5(i) = chi2(Obs,Exp5);
end;
DR = [D1(i) D2(i) D3(i) D4(i) D5(i)];
DR = DR/sum(DR);
DiffR(i,:,k) = DR;
end;
D_CI = []; % Estimate 95% confidence intervals for differences
for j = 1:5
    W(1,:) = DiffR(i,j,:);
    ci = bootci(W)';
    D_CI = [D_CI ci];
end;
DiffCI = [DiffCI;D_CI];
end;

if(doplot > 0) % Plots expected species abundance distributions
    figure;
    plot(Exp1);

```

```
    hold on;  
    plot(Exp2);  
    plot(Exp3);  
    plot(Exp4);  
    plot(Exp5);  
    plot(Obs,'r');  
end;  
  
return;
```