

Spatiotemporal variation in functional and taxonomic organization of stream-fish assemblages in central Texas

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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 comprise similar functional groupings despite phylogenetic differences. 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 organization; however, assemblages from different rivers but within the same season would be more similar to one another based on functional organization. I assessed functional and taxonomic organizations of fish assemblages from three tributaries of the Colorado River in Texas (Pedernales River, San Saba River, and South Llano River) across all four seasons. Direct ordination methods resulted in assemblages from the same river, regardless of season, clustering together. More specifically, the functional and taxonomic organizations of assemblages from the South Llano River, regardless of season, were noticeably different

than that from both the Pedernales River and the San Saba River, at least with respect to the first ordination axis. Current velocity, habitat availability, and temperature were influential in structuring the functional organization of assemblages in central Texas, while current velocity, substrate availability, and stream width were influential in structuring the taxonomic organization.

Keywords Functional organization · Stream fish · Taxonomic organization · Biodiversity

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 taxonomically defined species. This work has led to the formation of several important concepts. First, 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. Second, we realize that these determinants may result in assemblages in which species abundance and composition fluctuate through time (Starrett 1951; Grossman et al. 1982, 1990) or in assemblages in which the same species

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are found in roughly the same abundance over time (Smith and Powell 1971; Yant et al. 1984; Meffe and Minckley 1987). Third, we understand that the physical structure of a stream channel, in concert with flow regimes and energy input, produces a consistent pattern of structure along a stream (Vannote et al. 1980; Schlosser 1982; Matthews 1986; Pires et al. 1999; Hoeinghaus et al. 2003). However, recent emphasis has shifted from being taxonomic based on more of a functional perspective in which the traits of species are the primary focus (Goldstein and Meador 2004; Pont et al. 2006; Blanck et al. 2007; Higgins and Strauss 2008).

The functional organization of fish assemblages can be decomposed in a variety of ways depending on which species traits are examined and, of course, on what hypotheses are tested. For example, Schlosser (1982) classified fishes into trophic guilds, emphasizing the utilization of similar resources, in his examination of structure and function along habitat gradients. Others (Poff and Allan 1995; Angermeier and Winston 1999; Goldstein and Meador 2004) utilized a combination of species traits, such as trophic ecology, reproductive biology, substrate usage, geomorphic usage, locomotion, body morphology, and reproductive strategy. Hoeinghaus et al. (2006) incorporated life-history characteristics and trophic ecology in their examination of local and regional determinants of assemblage structure. Higgins and Strauss (2008) utilized a scheme proposed by Matthews (1998) that expanded traditional trophic groups to include the manner in which fishes affect ecosystem level processes by examining what fish eat, where they find food, and how they consume resources in their assessment of scale dependence in niche partitioning mechanisms among fish assemblages.

Although these and other studies (e.g., Balon 1975; Gatz 1979; Karr 1981) have contributed greatly to our understanding of the functional organization of stream-fish assemblages, particularly at varying spatial scales, they do not provide information on the temporal nature of functional organization and do not explicitly attempt to predict changes in functional diversity with environmental variables. Therefore, the objectives of this study were (1) to compare taxonomic and functional organization of assemblage structure among seasons and rivers and (2) to determine whether local environmental variables (e.g., temperature, current velocity, water depth,

substrate, stream width) serve as potential drivers for functional and taxonomic organization of stream-fish assemblages. 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 organization; however, assemblages from different rivers but within the same season would be more similar to one another based on functional organization. I formulated this hypothesis based on observations that species composition often changes among rivers, potentially a result of species-area and species-energy relationships (Oberdorff et al. 1995), or historical factors such as speciation and dispersal limitation (Tedesco et al. 2005). I expected any difference in species composition among locations to outweigh potential differences that may result within a single location over time. In terms of functional organization, different river systems appear to comprise similar functional groupings despite phylogenetic differences (Lamouroux et al. 2002). The relative abundance of these functional groups, however, might change as energy availability, hydrodynamics, prey availability, or temperature fluctuates over time; each of these environmental factors could differentially affect various functional attributes. For example, functional attributes based on life-history strategies respond to hydrodynamic forces but not to temperature or oxygen levels (Blanck et al. 2007).

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 more than 1,040 km and draining nearly 100,000 km² (Huser 2000). Three of the major tributaries of the Colorado River are the Pedernales, Llano, and San Saba Rivers, which enter the Colorado River from the west, are spring fed, and arise within the Edwards Plateau region (Brune 1975). The Colorado River supports approximately 90 species of freshwater fishes representing 20 families (generated from the TSNL Ecological Database Version 1.0). 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, Atherinopsidae, Catosomidae, Characidae, Cichlidae, Clupeidae, Cyprinodontidae, Esocidae, Fundulidae, Ictaluridae, Lepisosteidae, Moronidae, Mugilidae, 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 (spring, April 25–26 2003; summer, August 14–15 2003; fall, November 28–29 2003; and winter, February 28–29 2004). Each sampling site comprised one 100-m stretch of stream to provide a representative sample of the ichthyofauna. 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. For habitat data, I measured temperature ($^{\circ}\text{C}$), water depth (cm), and water velocity at 60% depth (m/s) and scored dominant substrate type (i.e., sand, gravel, cobble, boulder, bedrock) and habitat type (pool, riffle, run) at 120 randomly selected points distributed across the entire 100 m stretch of river. I also measured stream width at 10 m intervals along the 100 m stream reach and averaged them to produce a single estimate for each site. I inventoried fish assemblages at each site with a total of 120 min of backpack electrofishing distributed evenly over the sampling reach. I placed the captured fishes in five-gallon buckets containing MS-222. After sampling the entire stream reach, I placed the anesthetized fishes in 10% formalin to harden the tissues and to preserve the individuals until returning to the laboratory, where I identified, enumerated, and eventually stored the specimens in 70% ethanol.

Formation of functional groups

Although stream fishes can be partitioned into a variety of functional groups, I chose to use a scheme that incorporated trophic levels and life-history strategies. This scheme not only characterizes different aspects of assemblage structure than taxonomic organization

(Hoeinghaus et al. 2006), but life-history strategies are strongly associated with hydrodynamic forces (Blanck et al. 2007). For most species collected in this study, I gleaned functional classifications from the Appendix provided in Hoeinghaus et al. (2006). For the remaining species, I used the trophic classification provided in Linam and Kleinsasser (1998) and information provided in Winemiller (1992) and Winemiller and Rose (1992). All individuals of each species were classified into only one functional group (Hoeinghaus et al. 2006). The specific functional groups used in this study were herbivore-periodic, omnivore-equilibrium, omnivore-equilibrium/periodic, omnivore-periodic, piscivore-equilibrium, piscivore-equilibrium/periodic, invertivore-equilibrium, invertivore-opportunistic/equilibrium, invertivore-opportunistic, invertivore-opportunistic/periodic, and invertivore-periodic (Table 1).

Statistical analyses

I used canonical correspondence analysis (CCA) on $\log_{10}(x + 1)$ transformed 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 organization 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 CCA over correspondence analysis (Ter Braak 1986; Palmer 1993) 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 (Ter Braak 1986). Because environmental variables are standardized during the process of CCA (Palmer 1993), I chose not to standardize them prior to ordination analyses.

In addition to direct ordination, I statistically assessed the environmentally constrained site scores from the CCA for differences in mean values among rivers and among seasons. More specifically, I conducted a series of two-way analysis of variance without replication for functional and taxonomic organization with site scores from the first and second axes as dependent variables, and river and season as the factors of interest. I also conducted a series of two-way analysis of variance without replication for

Table 1 Temporal variation in species collected from three tributaries of the Colorado River of Texas

Scientific name	Code	Functional group	Pedernales River				San Saba River				South Llano River					
			Sp	Su	Fa	Wi	Sp	Su	Fa	Wi	Sp	Su	Fa	Wi		
<i>Ameiurus natalis</i> (Lesueur)	Amna	o-e											1			
<i>Campostoma anomalum</i> (Rafinesque)	Caan	h-p				2	51	6	5			9	31	5		
<i>Carpiodes carpio</i> (Rafinesque)	Caca	o-p			1											
<i>Cichlasoma cyanoguttatum</i>	Cicy	i-e									1	29	61	15		
<i>Cyprinella venusta</i> (Girard)	Cyve	i-op	43	14	77	19	529	177	241	185	6	1	26	11		
<i>Dionda nigrotaeniata</i> (Cope)	Dini	o-p			20		20				121	58	212	52		
<i>Etheostoma lepidum</i> (Baird and Girard)	Etle	i-oe	3		13	3	7	2	10	19	51	36	74	147		
<i>Etheostoma spectabile</i> (Agassiz)	Etspe	i-oe	1				1		12	11	38	28	79	36		
<i>Gambusia affinis</i> (Baird and Girard)	Gaaf	i-o	29	7	187	107	109	87	55	10	5	5	53	7		
<i>Ictalurus punctatus</i> (Rafinesque)	Icpu	o-ep	1	1	2	1		8	2		4	1	7	5		
<i>Lepomis auritus</i> (Linnaeus)	Leau	i-e	9		96	38	21	6	17	12	6	1	13	24		
<i>Lepomis cyanellus</i> (Rafinesque)	Lecy	p-ep	13	1	47	15		6	9	10	5		12	16		
<i>Lepomis gulosus</i> (Cuvier)	Legu	p-e	1	1	1						3					
<i>Lepomis macrochirus</i> (Rafinesque)	Lema	i-e	2	4	121	17	10	10	74	23	11		12	9		
<i>Lepomis megalotis</i> (Rafinesque)	Leme	i-e	13	4	72	31	27	11	85	35	15	2	13	6		
<i>Micropterus dolomieu</i> (Lacepede)	Mido	p-ep											1			
<i>Micropterus punctatus</i> (Rafinesque)	Mipu	p-ep			7	3		8	17	12		2				
<i>Micropterus salmoides</i> (Lacepede)	Misa	p-ep			1			1								
<i>Moxostoma congestum</i> (Baird and Girard)	Moco	i-p	2		9			1	2				8	1		
<i>Notropis amabilis</i> (Girard)	Noam	i-op					31		2	6	24		5	17		
<i>Notropis stramineus</i> (Cope)	Nost	i-op	1	10	75	8	195	3	25	18	1	2		6		
<i>Percina carbonaria</i> (Baird and Girard)	Peca	i-p	6		14	2	7		12	16	2		28	6		
<i>Pimephales vigilax</i> (Baird and Girard)	Pivi	i-op		4	36		24			1						
<i>Pylodictis olivaris</i> (Rafinesque)	Pyol	p-ep		1				1				1				

Species codes are formed from the first two letters each of the genus and species. *Abbreviations* for functional groups are formed from the first letter of the trophic guild and life-history strategy (Table 2). *Abbreviations* for seasons correspond to spring (*Sp*), summer (*Su*), fall (*Fa*), and winter (*Wi*)

each of the environmental variables as well. Because the analyses were without replication, I did not include an interaction term in the model. Statistical significance was assessed with an alpha level of 0.05.

Results

A total of 4,948 fish representing 24 species (Table 1) and 11 functional groups (Table 2) was collected across all four seasons and three localities. I collected a total of 20 species in the Pedernales River, 19 species in the San Saba River, and 21 species in the South Llano River. The numerically dominant species collected from the Pedernales River fauna were

mosquitofish *Gambusia affinis*, blacktail shiner *Cyprinella venusta*, bluegill sunfish *Lepomis macrochirus*, and longear sunfish *Lepomis megalotis*. The dominant functional groups collected from the Pedernales River fauna were invertivore-equilibrium, invertivore-opportunistic, and invertivore-opportunistic/periodic. The San Saba River fauna consisted primarily of blacktail shiner, mosquitofish, sand shiner *Notropis stramineus*, longear sunfish, and bluegill sunfish, with invertivore-opportunistic/periodic and invertivore-equilibrium, the most abundant functional groups. The most abundant species collected from the South Llano River were Guadalupe roundnose minnow *Dionda nigrotaeniata*, green-throat darter *Etheostoma lepidum*, orangethroat

Table 2 Temporal variation in functional groups collected from three tributaries of the Colorado River of Texas

Functional group	Code	Pedernales River				San Saba River				South Llano River			
		Sp	Su	Fa	Wi	Sp	Su	Fa	Wi	Sp	Su	Fa	Wi
Herbivore-periodic	h-p				2		51	6	5		9	31	5
Invertivore-equilibrium	i-e	24	8	289	86	58	27	176	70	33	32	99	54
Invertivore-opportunistic	i-o	29	7	187	107	109	87	55	10	5	5	53	7
Invertivore-opportunistic/equilibrium	i-oe	4		13	3	8	2	22	30	89	64	153	183
Invertivore-opportunistic/periodic	i-op	44	28	188	27	779	180	268	210	31	3	31	34
Invertivore-periodic	i-p	8		23	2	7	1	14	16	2		36	7
Omnivore-equilibrium	o-e									1			
Omnivore-equilibrium/periodic	o-ep	1	1	2	1		8	2		4	1	7	5
Omnivore-periodic	o-p			21		20				121	58	212	52
Piscivore-equilibrium	p-e	1	1	1						3			
Piscivore-equilibrium/periodic	p-ep	13	2	55	18	0	16	26	22	5	4	12	16

Abbreviations for functional groups are formed from the first letter of the trophic guild and life-history strategy. Abbreviations for seasons correspond to spring (*Sp*), summer (*Su*), fall (*Fa*), and winter (*Wi*)

Table 3 Mean environmental conditions for each of the sampling sites, with standard deviation in parentheses

Season	Width (m)	Temp (°C)	Depth (cm)	Velocity (m/s)	Substrate	Habitat
South Llano River						
Spring	20.43 (7.37)	23.32 (0.07)	47.62 (7.36)	3.00 (1.11)	3.68 (0.75)	2.70 (0.53)
Summer	19.19 (5.25)	28.42 (0.08)	34.28 (5.90)	2.88 (0.97)	3.72 (0.52)	2.49 (0.71)
Fall	21.88 (5.90)	15.00 (0.08)	36.68 (5.38)	4.14 (1.03)	3.83 (0.30)	2.57 (0.60)
Winter	22.37 (6.72)	15.28 (0.05)	35.32 (6.54)	3.13 (1.07)	3.68 (0.42)	2.49 (0.62)
San Saba River						
Spring	30.56 (7.19)	20.32 (0.13)	32.38 (9.53)	1.20 (1.38)	4.78 (0.40)	2.71 (0.53)
Summer	23.04 (11.78)	26.25 (0.18)	20.86 (6.49)	0.00 (0.00)	4.63 (0.56)	2.64 (0.60)
Fall	35.12 (6.24)	11.73 (0.15)	29.43 (6.66)	0.00 (0.00)	4.63 (0.57)	2.49 (0.74)
Winter	37.66 (3.40)	11.44 (0.04)	34.21 (9.83)	1.37 (1.13)	4.64 (0.62)	2.37 (0.73)
Pedernales River						
Spring	14.45 (3.47)	21.54 (0.08)	46.64 (10.46)	0.25 (0.31)	3.34 (0.60)	2.72 (0.66)
Summer	11.91 (2.39)	25.49 (0.08)	34.42 (5.75)	0.00 (0.00)	2.93 (0.43)	2.83 (0.50)
Fall	13.05 (3.03)	11.42 (0.10)	37.90 (5.16)	0.00 (0.00)	3.31 (0.61)	2.58 (0.77)
Winter	14.28 (3.09)	12.18 (0.02)	45.90 (5.77)	0.05 (0.05)	2.94 (0.63)	2.58 (0.77)

darther *Etheostoma spectabile*, and Rio Grande cichlid *Cichlasoma cyanoguttatum*; the functional organization consisted primarily of omnivore-periodic and invertivore-opportunistic/equilibrium.

Despite some seasonal variation in environmental parameters (Table 3), the results do not support my original hypothesis. That is, direct ordination methods (CCA) resulted in assemblages from the same river, regardless of season, clustering together. The functional (Fig. 1) and taxonomic (Fig. 2) organizations of

assemblages from the South Llano River, regardless of season, were noticeably different than assemblages from both the Pedernales River and the San Saba River, at least with respect to the first ordination axis. In fact, results from two-way analysis of variance without replication indicate site scores along the first axis were statistically different among rivers for both functional ($F = 67.6; df = 2; P < 0.000$) and taxonomic organization ($F = 73.4; df = 2; P < 0.000$); site scores along the second ordination axis were not

Fig. 1 Ordination results from CCA for functional organization of assemblages, with environmental variables presented as vectors. Functional group codes are formed from the first letter each of the tropic group and life-history strategy. *Closed black circles* represent the Pedernales River. *Open circles* represent the San Saba River. *Closed gray circles* represent the South Llano River. *Abbreviations* for seasons correspond to spring (*sp*), summer (*su*), fall (*fa*), and winter (*wi*)

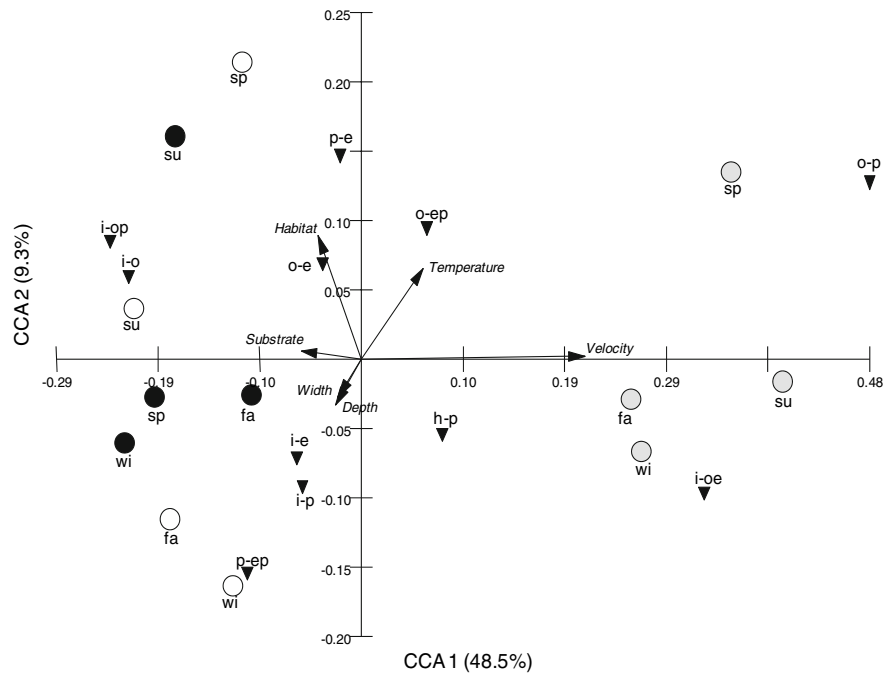
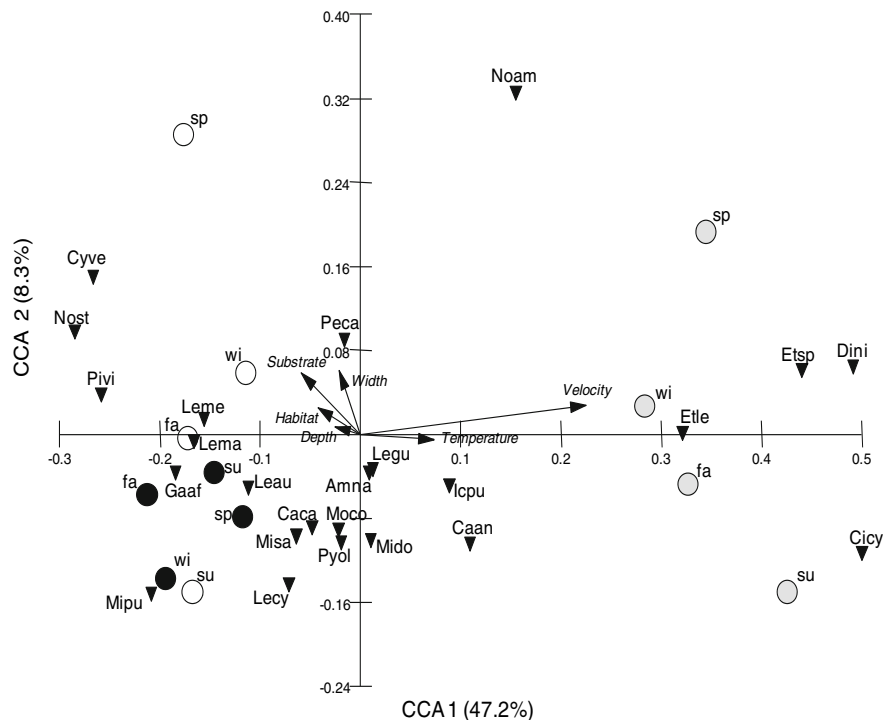


Fig. 2 Ordination results from CCA for taxonomic organization of assemblages, with environmental variables presented as vectors. Species codes are formed by the first two letters each of the genus and species. *Closed black circles* represent the Pedernales River. *Open circles* represent the San Saba River. *Closed gray circles* represent the South Llano River. *Abbreviations* for seasons correspond to spring (*sp*), summer (*su*), fall (*fa*), and winter (*wi*)



significantly different among rivers. The main environmental factor responsible for this separation was current velocity (functional organization: $r = 0.95$; taxonomic organization, $r = 0.93$). There were no

significant differences in site scores among seasons, regardless of which ordinated axis or method of organization was considered. However, there appears to be slight differences in functional organization

between spring/summer and fall/winter assemblages along the second ordination axis (Fig. 1) in which habitat availability and water temperature correlated highly ($r = 0.92$ and $r = 0.67$, respectively).

Discussion

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. Several possible explanations may account for this observed pattern. First, relative abundance of functional groups was not dependent on environmental factors. 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 (Poff and Allan 1995; Lamouroux et al. 2002; Goldstein and Meador 2004; Hoeinghaus et al. 2006; Higgins and Strauss 2008), it is the individuals that are responding to environmental conditions rather than the groups themselves. Second, individual fish modified their use of available resources. Many fishes change their feeding behavior (Miller 1979; Richard and Wainwright 1995; Hernandez 2000) and habitat use (Wakeling et al. 1999; Sagnes et al. 2000) during ontogeny. In addition, many adult fishes are opportunistic in both habitat use and diet selection due to environmental variation, which can cause a high degree of overlap in their ecological roles (Long and Fisher 2000). Third, seasonal changes in environmental conditions were not great enough to influence the functional organization of fish assemblages. Current velocity, which is a main environmental factor associated with life-history strategies (Blanck et al. 2007), did not significantly differ among seasons. It did, however, significantly differ among rivers and contribute to the functional and taxonomic organization of assemblages. Perhaps the hypothesis would hold in systems that have more pronounced seasonal variation in discharge.

Streams of the southwestern United States, including many of those found in Texas, are subjected to a wide array of environmental factors ranging from

severe droughts (Horwitz 1978) to flash flooding (Fisher et al. 1982). In addition, many of these streams are faced with environmental perturbations due to anthropogenic modifications including the construction of reservoirs (Wilde and Ostrand 1999) and current practices in the agriculture industry (Onstad et al. 1991). These environmental influences can affect the distribution and abundance of many stream fishes (Grossman et al. 1998). In this study, current velocity, habitat availability, and temperature were influential in structuring the functional organization of assemblages in central Texas, while current velocity, substrate availability, and stream width were influential in structuring the taxonomic organization. In fact, current velocity is one of the most widely reported factors responsible for structuring the taxonomic organization of stream-fish assemblages (Ross 1986). Environmental factors associated with hydrodynamics have even been shown to impose such enormous constraints on organisms, especially in lotic waters, that fish assemblages on different continents show strong similarities in functional organization (Lamouroux et al. 2002). However, environmental factors may only determine the presence or absence of a functional group and not the relative abundance of individuals within the group.

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 river 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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