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SUMMER FISH ASSEMBLAGES IN CHANNELIZED AND UNCHANNELIZED REACHES OF THE SOUTH SULPHUR RIVER, TEXAS

A Thesis

by

CHRISTINE CONNER BURGESS

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

August 2003

Major Subject: Wildlife and Fisheries Sciences

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Texas Water
Resources Institute
make every drop count

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Approved as to style and content by:

Frances P. Gelwick (Chair of Committee)	Kirk O. Winemiller (Member)
Anne Chin (Member)	Robert D. Brown (Head of Department)

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ABSTRACT

Summer Fish Assemblages in

Channelized and Unchannelized Reaches of

the South Sulphur River, Texas. (August 2003)

Christine Conner Burgess, B.S., Texas A&M University

Chair of Advisory Committee: Dr. Frances P. Gelwick

I used a conceptual model proposed by Schlosser (1987) to compare channelized and unchannelized reaches of the South Sulphur River, Texas. This model suggests that fish assemblage structure can be predicted based on the level of habitat heterogeneity, especially with regard to the level of pool development. Based on Schlosser's model, I hypothesized that habitat heterogeneity would be greater in the unchannelized (as compared to channelized) reach of the South Sulphur River, which would therefore have more stable fish assemblages. Fish assemblages in this reach would have similar total fish density and higher species richness, in addition to lower density and higher biomass of larger-bodied fish (primarily piscivores and omnivores), as well as lower density and biomass of juveniles and adults of small-bodied species (primarily invertivores) as compared to the channelized reach. Habitat characteristics conformed to my predictions, but fish assemblage attributes were opposite those hypothesized. Schlosser's study focused on biotic processes more than the abiotic effects of a highly variable, stochastic environment. I propose that abiotic processes, particularly extreme fluctuations in flow regimes, are likely to be the most influential factors affecting fish assemblages in the

South Sulphur River. Streams in this region are naturally subject to extreme variations in streamflow, but unchannelized sites may have been more directly influenced by water release or retention from the relatively recent construction of Cooper Dam located just upstream, whereas channelized sites, located much further downstream, were probably less affected. Most fish species present in the South Sulphur River are considered habitat generalists, have evolved to cope with extreme changes in environmental conditions, and are able to populate a variety of available habitats. Therefore, future management of this stream should reflect the needs of the few remaining fluvial specialists in this system, such as the intolerant freckled madtom and mimic shiner.

DEDICATION

This thesis is dedicated to my Mom and Dad. You have always encouraged me to pursue my interests and follow my dreams. Without your love and support, none of this would have been possible.

ACKNOWLEDGMENTS

I would like to thank my advisor, Fran Gelwick, for believing in me and molding me into a professional scientist. With your encouragement, I was able to achieve more than I thought was possible during my graduate education. You were always ready to provide help, a great source of ideas, and a one of a kind advisor and friend. I would also like to thank my committee members, Kirk Winemiller and Anne Chin, for providing ideas and insight into my project and for reviewing prior drafts of this thesis.

Without my field help, my project would not have gotten very far. Thanks to Fran Gelwick, Ray Li, Virginia Shervette, Suzanne Smith, and David Taylor for providing companionship and a helping hand in the field, frequently under less than desirable conditions. I would also like to thank the Texas Department of Transportation for helping us out of a jam, freeing our truck from the muddy banks of the Sulphur River. Funding for this project was provided by the Texas Water Development Board and the Texas Water Resources Institute.

Thanks to my fellow graduate students for serving as a source of ideas, support, and stress relief. I would especially like to thank Mike Morgan for compelling me to accomplish my goals. You are always there when I need an ear to listen, and always have good advice on how to overcome obstacles. You are very much like a big brother, always trying to make sure I learned from the mistakes of those that came before me.

Last but not least, I am extremely grateful to my family whose words of encouragement and belief that I could do anything that I put my mind to kept me going.

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INTRODUCTION

Channelization is the artificial straightening, widening, and/or deepening of stream channels. It can involve dredging, bank stabilization, and clearing or snagging operations and has been widely practiced in the United States and the United Kingdom (Schneberger and Funk 1971; Brookes and Gregory 1983; Brooks 1987, 1988). Streams are channelized to increase land drainage, enhance agricultural production, and provide flood control (Best et al. 1978). Such environmental disturbance can lead to increases in water temperature, erosion, channel incision, and sediment transport (Shields et al. 1994, 1998). Channelization causes "flashier" hydrographs (Campbell et al. 1972; Shankman and Pugh 1992; Shields and Cooper 1994; Woltemade and Potter 1994; Wyzga 1996), as well as loss of instream and bankside habitat, with subsequent changes in aquatic populations and communities (Trautman and Gartman 1974, Duvel et al. 1976; Brookes and Gregory 1983; Cowx et al. 1986; Brookes 1988). Fish habitat in a channelized stream reach has been commonly characterized as having less total area (Chapman and Knundsen 1980), higher stream gradient and velocity, finer and less stable substrata (Zimmer and Bachmann 1978), absence of alternating pools and riffles, and overall reduced heterogeneity of habitat features (Hortle and Lake 1983; Schlosser 1987). Channelization and construction of levees can disrupt processes associated with a natural flood regime. Productivity of floodplain rivers directly depends on connectivity of the

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main channel to its backwaters (Amoros and Roux 1988) and on periodic flooding (Holcík and Bastl 1976). Backwaters, oxbow lakes, and inundated riparian habitats are important spawning and nursery areas for many riverine fish (Holland 1986; Copp 1989; Winemiller et al. 2000) and provide refuge when conditions within the main river are unfavorable, such as during pollution events and high-velocity spates (Holcík and Bastl 1976).

Several studies document effects of channelization on fish communities (Schneberger and Funk 1971; Huggins and Moss 1975; Stern and Stern 1980a, b; Schlosser 1982a, b, 1987; Lyons and Courtney 1989). Although ecologists realize that processes related to both physical disturbance and biotic interactions influence community organization (Sousa 1984b), their conclusions differ regarding the relative importance of abiotic versus biotic processes that regulate assemblage structure of fishes in particular streams (Schoener 1987). Some investigators have emphasized the importance of temporal variability and the significance of environmental stochasticity (Grossman et al. 1982), whereas others have reported relatively stable fish assemblages (Moyle and Vondracek 1985) characterized by strong biotic interactions (Fraser and Cerri 1982; Power and Matthews 1983). Moreover, spatial heterogeneity, frequency and intensity of physical disturbances, and life history attributes of stream biota must be considered (Connell 1975, 1978; Sousa 1979, 1984a, b; Strong 1983; Karr and Freemark 1983, 1985; Wiens 1984).

One widely referenced conceptual framework (Figure 1) for stream-fish assemblage structure (based on Jordan Creek, Illinois) emphasizes the importance of

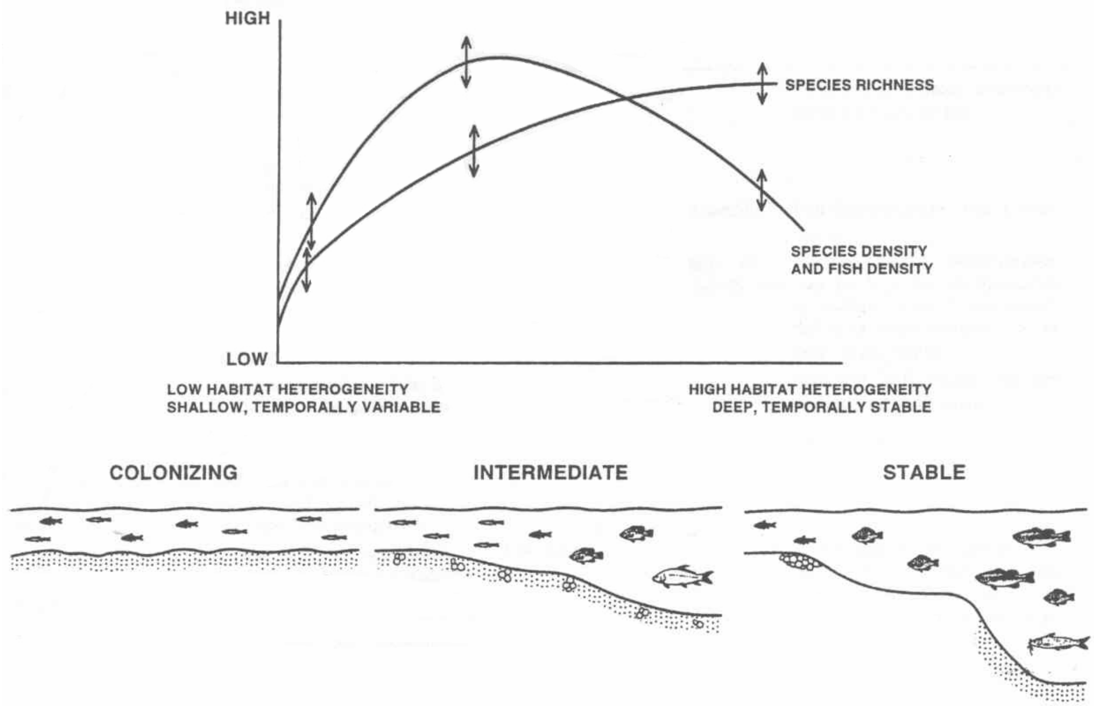

FIGURE 1.? Conceptual model for fish communities in warmwater streams along a gradient of an increasing level of pool development (Schlosser 1987).

habitat heterogeneity—in particular, pool development, as it is linked to habitat volume—as a key factor determining spatial and temporal assemblage stability (Schlosser 1987). Uniform habitat (i.e., poorly developed pools, having relatively low habitat heterogeneity, shallow water, and low habitat volume) results in a simple and more unstable assemblage. In North America, shallow, uniform habitats contain mostly "colonizing" species dominated by cyprinids. These assemblages are dominated by those species having rapid maturity, prolonged breeding seasons, high reproductive rates, and young with strong dispersal capability. Simple trophic complexity and predominance of younger age classes lead to competition, rather than predation, as the critical biological influence on assemblage dynamics (Schlosser 1987). Persistent deep habitats apparently are needed by older age classes and larger-bodied pool species in order to avoid shallow areas where space is limited and risk from terrestrial predators is higher (Power 1984; Harvey and Stewart 1991).

The extent of pool development directly relates to both habitat heterogeneity and habitat volume (Figure 1). As the level of pool development increases, so does species richness, but at a slower rate, because younger age classes of most pool species are already included in the assemblage. In North American streams, greater pool development changes the age (size) structure, species composition, and trophic structure of the assemblage due to a pronounced shift toward fewer, larger centrarchids (most of which are piscivores) and catostomids (most of which are benthic invertivores). Therefore, predation becomes a critical biotic interaction for most small-bodied species in well-developed pool habitat. As predators increase, cyprinid abundance decreases and their average body size increases. Predation is less important in determining distribution and abundance of larger (older) fishes because size is an effective refuge from predation (Werner et al. 1983; Werner and Gilliam 1984). Instead, competition and habitat-related differences in foraging efficiency are critical to large individuals in well-developed pool habitats (Werner and Hall 1976, 1977, 1979; Mittlebach 1981; Werner and Gilliam 1984). Compared to assemblage composition in shallow and poorly developed pools, assemblages in well-developed pools are relatively more "stable" over time because small-bodied cyprinids and juveniles of larger species comprise a comparatively smaller component, thus reducing the influence of seasonal fluctuations and recruitment. In addition, deeper pools provide a more stable refuge from extreme conditions during harsh winters and summer low-flows, which subsequently reduce the importance of emigration, mortality, and recolonization (Schlosser 1987). Although physical and biological components of streams are more stable in reaches with larger, more well-developed pools, periods of drought and flooding can still create major (albeit temporary) shifts in assemblage patterns (Matthews 1986; Schlosser 1990).

I compared fish assemblages in channelized versus unchannelized reaches of the South Sulphur River, Texas sampled during summer low-flow conditions in each of two consecutive years. Hereafter, I define an assemblage (c.f. Matthews 1998) as comprising fishes found together in one particular place or "locality" and a locality as a place included in a typical sample such that individual fishes have at least a reasonable chance of encountering each other during normal daily activities, although some may be more nocturnal than diurnal (Helfman 1981). Fish assemblages can be characterized by attributes such as species richness, species density, total density of individuals, trophic structure, and life history stages. Habitat characteristics include physical heterogeneity of depth, velocity, and substrate size, and assessment of overall quality relative to a reference condition. In particular, I described (1) habitat characteristics, (2) fish assemblage structure, 3) fish-habitat relationships, and compared the results of this study to patterns expected from ecological theory and published results from other streams. Based on Schlosser's model of Jordan Creek (Schlosser 1987), I hypothesized that habitat heterogeneity would be greater in the unchannelized (as compared to channelized) reach of the South Sulphur River, which would therefore have more stable fish assemblages. Fish assemblages in this reach would have similar total fish density and higher species richness, in addition to lower density and higher biomass of larger-bodied fish (primarily piscivores and omnivores), as well as lower density and biomass of juveniles and adults of small-bodied species (primarily invertivores) as compared to the channelized reach.

STUDY AREA

The Sulphur River Basin is located in northeast Texas. Flowing eastward from its headwaters in the North, Middle, and South Sulphur Rivers to its main channel confluence with the Red River in Arkansas, it drains approximately 9100 km^2. Impoundments include Cooper Lake on the South Sulphur River, and Wright Patman Lake on the main channel just west of the Texas-Arkansas border. The western half of the basin comprises the Texas Blackland Prairie ecoregion and the eastern half comprises the South Central Plains ecoregion (Omernik 1987). Bottomland hardwood forest within the upper region of the basin is concentrated along the South Sulphur River. The remaining areas, which were historically logged, include farm and pasture lands. Crops include cotton, soybeans, grain sorghum, corn, wheat, peanuts, alfalfa, and hay. Livestock consist primarily of beef and dairy cattle and poultry (Ressel 1979).

The upper half of the Sulphur River Basin was extensively channelized (but not lined by concrete) in an attempt to alleviate the flooding of farmland (Figure 2). The entire North Sulphur River and a small section of the upper main stem were channelized in the 1930's. In the 1950's the lower third of the South Sulphur River was channelized, straightened, and moved north of its original location. The old channel of the South Sulphur River still exists, but it remains dry for much of the year, and a levee currently blocks any connection to the newer channel.

A reservoir is proposed for the South Sulphur River downstream of Cooper Lake, and in consideration of possible mitigation for its construction, the fishes and their use of

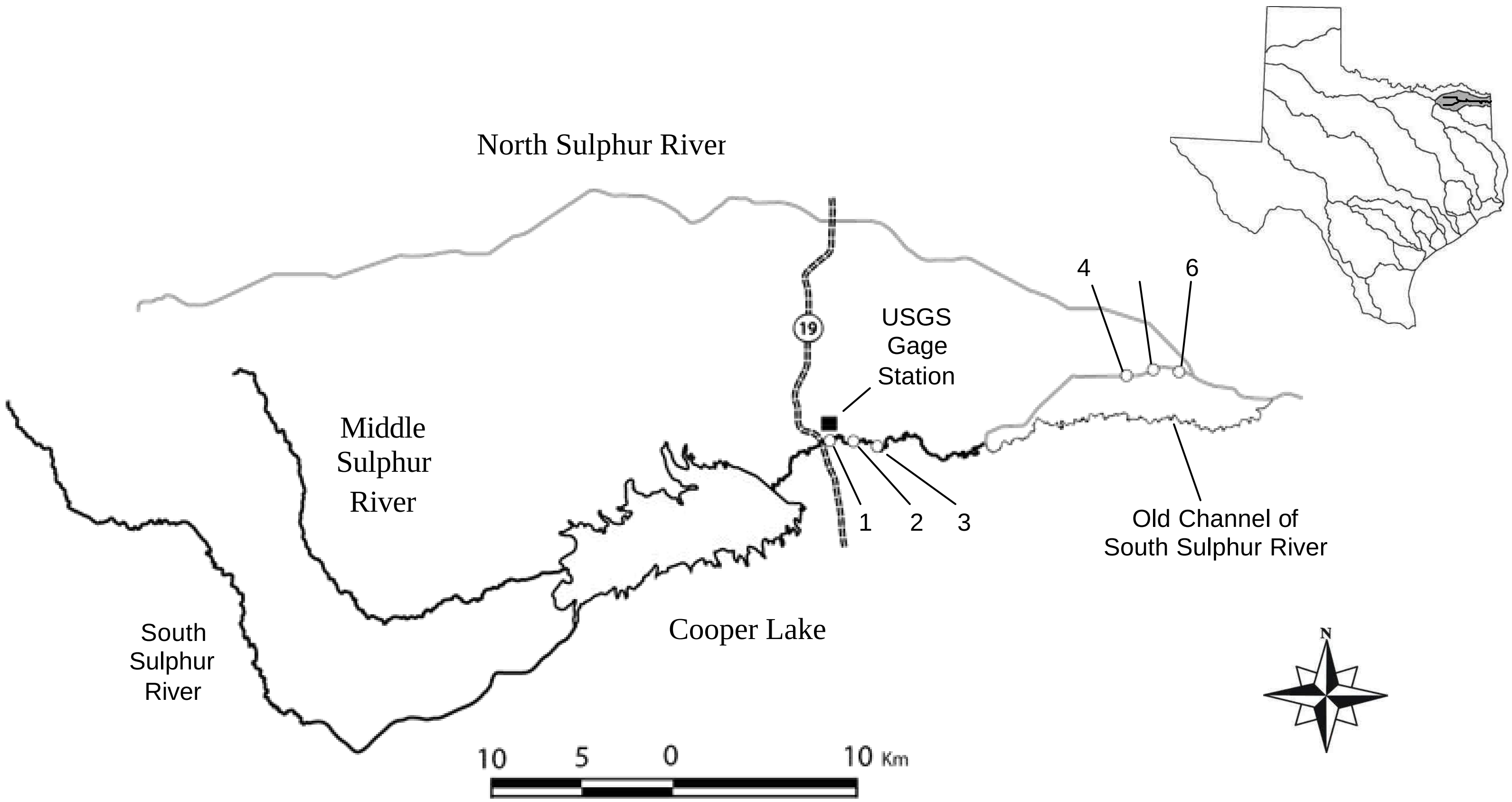

FIGURE 2.? Map of the western half of the Sulphur River Basin showing the location of sites sampled during August 2001 and July 2002. Channelized reaches are displayed in gray.

river habitats must be documented. Due to its remote location (few roads or river access points), fish assemblages within the South Sulphur River have not been adequately studied. Only a few studies are available that historically document fish species from the Sulphur River Basin such as Bonn & Inman (1955), Carroll et al. (1977), Turner (1978), Capone and Kushlan (1991). However, several studies have been recently completed that document fish assemblages and their relationships to available habitat including Gelwick and Morgan (2000), Morgan (2002), and Gelwick and Burgess (2002).

METHODS

Site and Habitat Identification

Three representative sites were selected as replicate samples in the unchannelized reach (sites 1, 2, and 3) and three in the channelized reach (sites 4, 5, and 6) of the South Sulphur River based upon access (Figure 2). Habitats within each site were categorized based on hydraulic characteristics into one of the four following mesohabitat types: pools, runs, riffles, and backwater areas. Definitions for mesohabitats are as follows: pools may vary in depth and be flowing, but have a smooth surface; runs vary in depth but generally up to 50% of their water surface is turbulent, or wavy, whereas in riffles >50% of the surface is turbulent (Jowett 1993); and backwaters have little or no flow, and are still connected, but adjacent to the main channel. Site length was equivalent to 20 times the wetted stream width at base flow in order to encompass the habitat types present within each reach. Mean daily discharges were obtained from USGS gage number 07342500 (South Sulphur River near Cooper, Texas). Samples were obtained during relatively stable low-flow conditions. Low-flow conditions are important limiting factors for stream fishes that test the ability of fishes to persist through harsh environmental conditions (Stalnaker 1981), and thus influence the stability of assemblage structure. Low-flow periods have been reported to cause the greatest spatial variation of stream-fish assemblages because habitat diversity is also at its highest due to a variety of riffle, pool, and run habitats (Gido et al. 1997).

Fish Collection

Fishes were collected in two consecutive years during summer low-flow conditions, which can limit survival rates. Three gear types were used; straight seines, gill nets, and electrofishers. All sampling was conducted during daylight hours, except gill nets that were left overnight. Straight seines of 5-mm mesh were 1.2 m deep and 2.4 m, 3.0 m, or 6.1 m long, as appropriate for the habitat that was sampled. One 38.1-m long experimental gillnet (five panels, each 7.6 m long x 1.8 m deep with 2.5, 3.8, 5.1, 6.3, and 7.6 cm bar mesh) was set at each site in deeper pools and angled diagonally from bank to bank in an effort to maximize flow interception by all panels. Pools chosen for gill nets were deep enough to permit the fullest possible extension of the net. Nets were fished for a minimum of 4 hours. A 4.2-m long, aluminum jon boat powered by a 15-horsepower outboard motor was equipped for electrofishing with a Coffelt control box, a handheld probe, and powered by a 3000 watt Honda generator. Direct current (DC) output was set at 200-350 V to achieve 3-5 A depending on conductivity. Electrofishing was conducted in an upstream direction.

Total fishing effort at a site continued until at least 20% of each available mesohabitat type was sampled (Vadas and Orth 1998) and no additional new species were collected in 3 consecutive seine hauls, or 3 consecutive 5-minute periods of electrofishing in each mesohabitat. Fishes greater than 100 mm were identified, counted, weighed (nearest 1 g), total length recorded (nearest 1 mm), and released in the field. Voucher specimens, and small or uncommon fishes were preserved in 10% formalin, transported to the lab for identification, and counted. Specimens transported to the lab were washed out of formalin, preserved in 70% ethyl alcohol, and deposited in the Texas Cooperative Wildlife Collection at Texas A&M University.

Habitat Characteristics

Habitat Heterogeneity

Sampling protocol and calculation of habitat heterogeneity followed Gorman and Karr (1978) with slight modifications. Habitat was measured at 1-m intervals along each of six across-stream transects spaced equidistant along the site. Three variables related to habitat heterogeneity were measured: depth, current, and substrate type (Table 1). Habitat heterogeneity was calculated using the Shannon-Weiner equation for each variable independently and added them together for a combined index of habitat heterogeneity (H_{DCS}). Gorman and Karr (1978) found that a combination of these three habitat variables are most appropriate for estimating fish species diversity over a wide range of stream physiographies and fish groups. Depth (nearest 0.1 m) was measured using a graduated wading rod. Current was measured at 0.6 depth with a Marsh-McBirney Model 2000 digital flowmeter. Habitat heterogeneity was only measured during summer 2002; therefore, a one-way analysis of variance was used to test differences in heterogeneity between channelized and unchannelized reaches. Significance was based on $P_{\alpha} \leq 0.05$ for all tests.

Habitat Quality

Evaluation of habitat quality followed the metrics of Barbour et al. (1999) for

TABLE 1.? Descriptions of categories for each habitat variable used in measuring stream habitat heterogeneity (modified from Gorman and Karr 1978).

		Category						
Variables		1	2	3	4	5	6	7
Depth (H_D)	Range (cm)	0-5	6-20	21-50	51-100	>100		
	Description	Very shallow	Shallow	Moderate	Deep	Very deep		
Current (H_C)	Flow Velocity (m/s)	<.05	.05-.2	.2-.4	.4-1.0	>1.0		
	Description	Very slow	Slow	Moderate	Fast	Torrent		
Substrate (H_S)	Diameter (mm)	<.01	.01-.05	.05-2	2-30	30-250	>250	
	Description	Clay	Silt	Sand	Gravel	Cobble	Boulder	LWD

low-gradient streams (Table 2). Individual instream and riparian metrics were scored, and then scores were combined to obtain an overall habitat quality score. Because this was done only during summer 2001, a one-way analysis of variance was used to test for differences between channelized and unchannelized reaches. In addition, I ran a Principal Components Analysis (PCA) of sites based on scores for each habitat quality metric to determine which metrics most influenced the overall score for each site. A PCA fits straight lines and planes by least-squares regression for multivariate data in such a way that the most important gradients for a sample are identified (Jongman 1995).

Fish Assemblage Structure

Univariate Analyses

A repeated measures analysis of variance was used to test differences between channelized and unchannelized reaches across both years for species richness, total fish density, number of tolerant species, and an Index of Biotic Integrity (IBI). For all tests, significance was based on $P_{\alpha} \leq 0.05$. Analyses used data from all gears, except gill nets were excluded from analysis of the IBI. Standardized catch for gill net samples was calculated as number per hour fished, and for seining and electrofishing as number per area sampled (m^2). Then, the proportion of the standardized catch in each gear was calculated in order for each gear type to have equal weight in analyses (Weaver et al. 1993). The IBI was used to test relative "health" of each reach based on particular characteristics of the fish assemblage (Karr et al. 1986). Metrics used for the IBI (Table 3) were developed from representative streams in this ecoregion (Linam et al. 2002).

TABLE 2.? Scoring criteria for habitat quality assessment of wadeable streams and rivers (Barbour et al. 1999).

Habitat Metrics	Condition Category			
	Optimal	**Suboptimal**	**Marginal**	**Poor**
1. Epifaunal Substrate/ Available Cover	Greater than 50% of substrate favorable for epifaunal colonization and fish cover; mix of snags, submerged logs, undercut banks, cobble or other stable habitat and at stage to allow full colonization potential (i.e., logs/snags that are not new fall and not transient).	30-50% mix of stable habitat; well-suited for full colonization potential; adequate habitat for maintenance of populations; presence of additional substrate in the form of newfall, but not yet prepared for colonization (may rate at high end of scale).	10-30% mix of stable habitat; habitat availability less than desirable; substrate frequently disturbed or removed.	Less than 10% stable habitat; lack of habitat is obvious; substrate unstable or lacking.
SCORE	20 19 18 17 16	15 14 13 12 11	10 9 8 7 6	5 4 3 2 1 0
2. Pool Substrate Characterization	Mixture of substrate materials, with gravel and firm sand prevalent; root mats and submerged vegetation common.	Mixture of soft sand, mud, or clay; mud may be dominant; some root mats and submerged vegetation present.	All mud or clay or sand bottom; little or no root mat; no submerged vegetation.	Hard-pan clay or bedrock; no root mat or vegetation.
SCORE	20 19 18 17 16	15 14 13 12 11	10 9 8 7 6	5 4 3 2 1 0
3. Pool Variability	Even mix of large-shallow, large-deep, small-shallow, small-deep pools present.	Majority of pools large-deep; very few shallow.	Shallow pools much more prevalent than deep pools.	Majority of pools small-shallow or pools absent.
SCORE	20 19 18 17 16	15 14 13 12 11	10 9 8 7 6	5 4 3 2 1 0
4. Sediment Deposition	Little or no enlargement of islands or point bars and less than <20% of the bottom affected by sediment deposition.	Some new increase in bar formation, mostly from gravel, sand or fine sediment; 20-50% of the bottom affected; slight deposition in pools.	Moderate deposition of new gravel, sand or fine sediment on old and new bars; 50-80% of the bottom affected; sediment deposits at obstructions, constrictions, and bends; moderate deposition of pools prevalent.	Heavy deposits of fine material, increased bar development; more than 80% of the bottom changing frequently; pools almost absent due to substantial sediment deposition.
SCORE	20 19 18 17 16	15 14 13 12 11	10 9 8 7 6	5 4 3 2 1 0
5. Channel Flow Status	Water reaches base of both lower banks, and minimal amount of channel substrate is exposed.	Water fills >75% of the available channel; or <25% of channel substrate is exposed.	Water fills 25-75% of the available channel, and/or riffle substrates are mostly exposed.	Very little water in channel and mostly present as standing pools.
SCORE	20 19 18 17 16	15 14 13 12 11	10 9 8 7 6	5 4 3 2 1 0

TABLE 2.? Continued.

Habitat Metrics	**Condition Category**			
	Optimal	**Suboptimal**	**Marginal**	**Poor**
6. Channel Alteration	Channelization or dredging absent or minimal; stream with normal pattern.	Some channelization present, usually in areas of bridge abutments; evidence of past channelization, i.e., dredging, (greater than past 20 yr) may be present, but recent channelization is not present.	Channelization may be extensive; embankments or shoring structures present on both banks; and 40 to 80% of stream reach channelized and disrupted.	Banks shored with gabion or cement; over 80% of the stream reach channelized and disrupted. Instream habitat greatly altered or removed entirely.
SCORE	20 19 18 17 16	15 14 13 12 11	10 9 8 7 6	5 4 3 2 1 0
7. Channel Sinuosity	The bends in the stream increase the stream length 3 to 4 times longer than if it was in a straight line. (Note - channel braiding considered normal in coastal plains and other low-lying areas. This parameter is not easily rated in these areas.)	The bends in the stream increase the stream length 1 to 2 times longer than if it was in a straight line.	The bends in the stream increase the stream length 1 to 2 times longer than if it was in a straight line.	Channel straight; waterway has been channelized for a long distance.
SCORE	20 19 18 17 16	15 14 13 12 11	10 9 8 7 6	5 4 3 2 1 0
8. Bank Stability (score each bank) Note: determine left or right side by facing downstream.	Banks stable; evidence of erosion or bank failure absent or minimal; little potential for future problems. <5% of bank affected.	Moderately stable; infrequent, small areas of erosion mostly healed over. 5-30% of bank in reach has areas of erosion.	Moderately unstable; 30-60% of bank in reach has areas of erosion; high erosion potential during floods.	Unstable; many eroded areas; "raw" areas frequent along straight sections and bends; obvious bank sloughing; 60-100% of bank has erosional scars.
SCORE___(LB)	Left Bank 10 9	8 7 6	5 4 3	2 1 0
SCORE___(RB)	Right Bank 10 9	8 7 6	5 4 3	2 1 0
9. Vegetative Protection (score each bank)	More than 90% of the streambank surfaces and immediate riparian zone covered by native vegetation, including trees, understory shrubs, or nonwoody macrophytes; vegetative disruption through grazing or mowing minimal or not evident; almost all plants allowed to grow naturally.	70-90% of the streambank surfaces covered by native vegetation, but one class of plants is not well represented; disruption evident but not affecting full plant growth potential to any great extent; more than one-half of the potential plant stubble height remaining.	50-70% of the streambank surfaces covered by vegetation; disruption obvious; patches of bare soil or closely cropped vegetation common; less than one-half of the potential plant stubble height remaining.	Less than 50% of the streambank surfaces covered by vegetation; disruption of streambank vegetation is very high; vegetation has been removed to 5 centimeters or less in average stubble height.
SCORE___(LB)	Left Bank 10 9	8 7 6	5 4 3	2 1 0
SCORE___(RB)	Right Bank 10 9	8 7 6	5 4 3	2 1 0
10. Riparian Vegetative Zone Width (score each bank riparian zone)	Width of riparian zone >18 meters; human activities (i.e., parking lots, roadbeds, clear-cuts, lawns, or crops) have not impacted zone.	Width of riparian zone 12-18 meters; human activities have impacted zone only minimally.	Width of riparian zone 6-12 meters; human activities have impacted zone a great deal.	Width of riparian zone <6 meters: little or no riparian vegetation due to human activities.
SCORE___(LB)	Left Bank 10 9	8 7 6	5 4 3	2 1 0
SCORE___(RB)	Right Bank 10 9	8 7 6	5 4 3	2 1 0

TABLE 3.—Index of Biotic Integrity metrics (Linam et al. 2002) used for evaluating assemblage structure in the South Sulphur River, Texas.

	Metric	Scoring Criteria		
		5	3	1
1	Total number of fish species	See Figure 3		
2	Number of native cyprinid species	>3	2-3	<2
3	Number of benthic invertivore species	>1	1	0
4	Number of sunfish species	>3	2-3	<2
5	% of individuals as tolerant species (excluding western mosquitofish)	<26%	26-50%	>50%
6	% of individuals as omnivores	<9%	9-16%	>16%
7	% of individuals as invertivores	>65%	33-65%	<33%
8	% of individuals as piscivores	>9%	5-9%	<5%
9	Number of individuals in sample			
	a. Number of individuals/seine haul	>87	36-87	<36
	b. Number of individuals/min electrofishing	>7.1	3.3-7.1	<3.3
10	% of individuals as non-native species	<1.4%	1.4-2.7%	>2.7%
11	% of individuals with disease or anomaly	<0.6%	0.6-1%	>1%
	AQUATIC LIFE USE:			
	= 49 Exceptional			
	41-48 High			
	35-40 Intermediate			
	< 35 Limited			

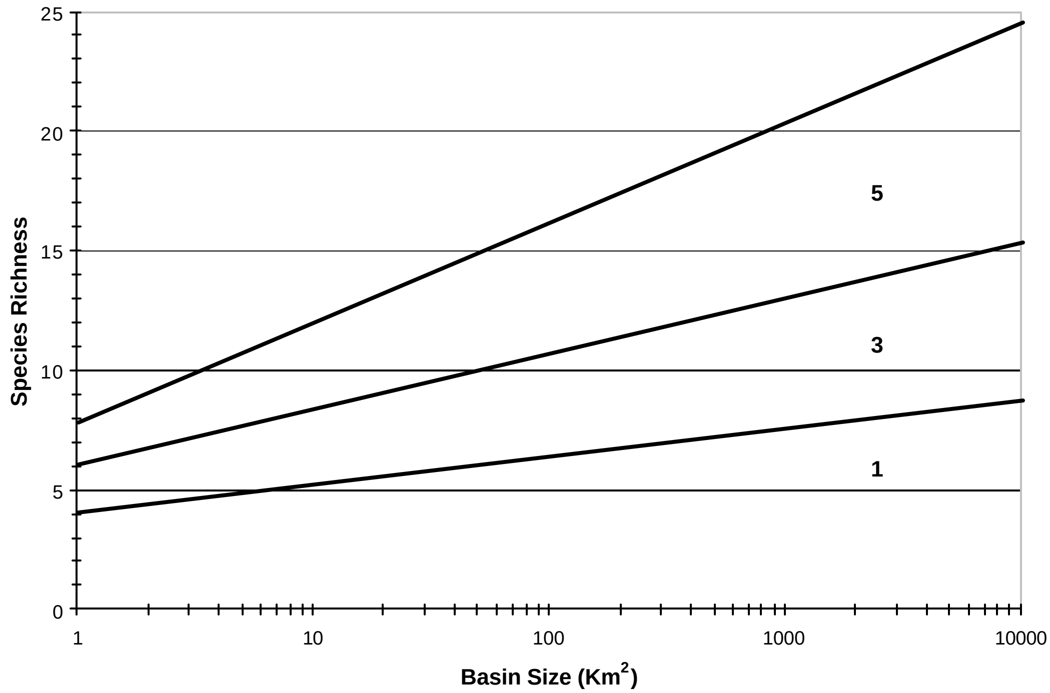

FIGURE 3.? Relationships between fish-species richness versus drainage basin size used to calculate the scores for metric number 1 in the Index of Biotic Integrity (Linam et al. 2002) for the South Sulphur River.

Trophic status and tolerance/intolerance categories were assigned following Linam and Kleinsasser (1998).

Multivariate Analyses

Relativization of standardized catch data followed that previously described for fish density. Following Weaver et al. (1993), 'species' were considered as separate gear-species combinations (e.g., gill netted, electrofished, and seined bluegill were considered as three separate species) in the analysis. All multivariate analyses followed Jongman et al. (1995). Because fish species collected in low abundance cannot be characterized accurately, only common species (those that made up greater than 1% of the total catch for each gear type) were included in all multivariate analyses. For analyses that distinguished between juveniles and adults, I used the length at which a species becomes sexually mature (Carlander 1969, 1977; Lee et al.1980; Robison and Buchanan 1988).

Correspondence Analysis.—Correspondence analysis (CA) is an indirect gradient analysis used to quantify the variation in relative abundance of species across collections. In my study, I used CA to describe spatial differences in both years between channelized and unchannelized reaches for assemblages based on (1) relative density of each species and (2) relative biomass of each species. For species density, four separate analyses were run—one each at the mesohabitat and site levels of spatial scale, and each of these based first on species, and second on juvenile and adult life-history stages of these species. For the analysis based on biomass, species were also categorized as one of four trophic groups: herbivore, invertivore, piscivore, or omnivore. Trophic classification was based on Linam and Kleinsasser (1998).

Multivariate Analysis of Variance with Repeated Measures.—The distribution of trophic-group biomass across reach and year was tested using multivariate analysis of variance with repeated measures (MANOVAR) following guidelines in Potvin and Lechowicz (1990). For this analysis, the relative biomass of all species was averaged across all gears. Proportions were arcsin transformed for analysis. Because it is most robust to assumptions of multivariate tests, Pillai's Trace was used to test within-subjects effects. Across the three trophic groups, linear contrasts were tested for main effect of reach, and for repeated measures, effects of year and reach by year interaction. Significance tests were based on $P_{\alpha} \leq 0.05$.

Canonical Correspondence Analysis.—Canonical correspondence analysis (CCA) is a direct gradient analysis that selects the linear combinations of environmental variables that are most strongly correlated with the dispersion of the dependent variables among samples (Jongman et al. 1995). In my study, the relative density of fish species was used to quantify the variation in assemblage structure that could be explained by (correlated with) habitat variables measured at each site. Environmental variables included reach (channelized or unchannelized) and mesohabitat type (pool, riffle, run, backwater) as categorical variables, and habitat quality score as a quantitative variable. A partial CCA was used to partition the variation explained in the CCA (Jongman et al. 1995) into that attributed to target variables, or variable groups (reach and mesohabitat type). By including all non-target variables as covariables in the analysis, the variance explained by non-target variables was removed along with that shared with (equally explainable by) the target variable. Thus, the residual variance explained by the target variable was the portion purely attributable to it in the CCA. Monte Carlo randomization (199 trials) was used to test the significance of the relationship between environmental variables and species distributions. The randomization trials were based on a repeated measures model. Significance tests were based on $P_{\alpha} \leq 0.05$.

Indicator Species Analysis.—In addition to canonical ordination, I used indicator species analysis (ISA) to determine which species and life-history stages were indicators of each of the four types of mesohabitats and two reaches. Therefore, four separate analyses were run, similar to those for CA. Higher indicator values are positively related to higher abundance and higher frequency of occurrence in samples. Significance of values were tested using proportions of Monte Carlo randomized trials (1000) having indicator values equal to or exceeding those observed. Significance tests were based on $P_{\alpha} \leq 0.05$.

RESULTS

Habitat Characteristics

Actual mean daily discharge during summer 2001 remained steady at 0.2 cms and ranged from 0.2-2.4 cms during summer 2002 (Figure 4). Mesohabitat types present at each site during each year are shown in Table 4. Unchannelized sites had a greater variety of mesohabitats, which collectively included all types categorized (pool, riffle, run, and backwater). Habitats in channelized sites were comprised of pools almost exclusively, except for one run observed at site 4 in summer 2002.

Habitat Heterogeneity

Channelized pools were more uniform in channel width, depth, and current than unchannelized pools. Overall H_{DCS} was greater in the unchannelized (3.00 ± 0.15 SE) than channelized reach (2.10 ± 0.15 SE), and of the three metrics, depth appeared to contribute most to the difference. Mean value for depth categories ranged from moderate to deep for all sites. Heterogeneity of depth was higher in the unchannelized (1.37 ± 0.05 SE) versus the channelized reach (1.14 ± 0.05 SE) (Table 5). There was no difference in the diversity of water velocity (very slow) or substrate type (silt) for either reach.

Habitat Quality Assessment

Overall habitat quality was higher in unchannelized (126.0 ± 2.06 SE) than in

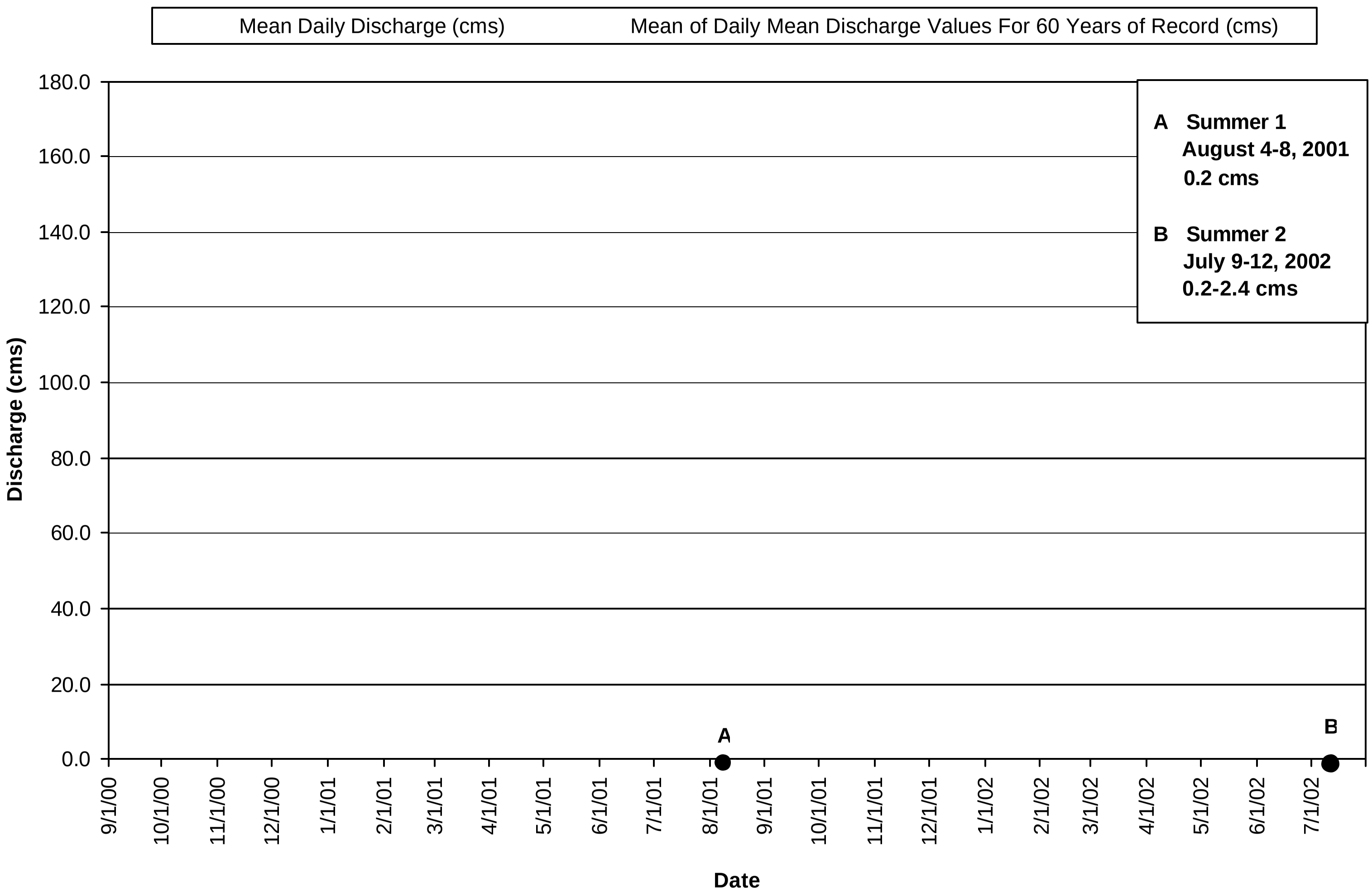

FIGURE 4.? Mean daily discharge recorded from September 1, 2000 to July 31, 2002, just before and during the study period at USGS gauge number 07342500 (South Sulphur River near Cooper, TX).

TABLE 4.? Presence of mesohabitat types in sites 1-6 in channelized and unchannelized reaches during summer 2001 and summer 2002.

	Summer 2001						Summer 2002					
	Unchannelized			Channelized			Unchannelized			Channelized		
Mesohabitat	1	2	3	4	5	6	1	2	3	4	5	6
Pool	x	x	x	x	x	x	x	x	x	x	x	x
Run	x	x	x	-	-	-	x	x	x	x	-	-
Riffle	x	-	x	-	-	-	x	-	-	-	-	-
Backwater	-	-	x	-	-	-	-	-	x	-	-	-

TABLE 5.? Summary of habitat heterogeneity, mean category score and its corresponding description for each habitat variable.

		Unchannelized			Channelized		
Variable		1	2	3	4	5	6
Depth	H_D	1.48	1.24	1.40	1.13	1.13	1.14
	Mean	3.5	2.9	3.3	2.7	3.3	3.5
	Description	Deep	Moderate	Moderate	Moderate	Moderate	Deep
Current	H_C	0.81	0.78	0.44	0.57	0.00	0.00
	Mean	1.4	1.4	1.2	1.3	1.0	1.0
	Description	Very slow	Very slow	Very slow	Very slow	Very slow	Very slow
Substrate	H_S	0.85	0.93	1.07	0.74	0.94	0.62
	Mean	1.5	1.7	2.0	1.7	1.8	1.7
	Description	silt	silt	silt	silt	silt	silt
TOTAL	H_{DCS}	3.14	2.95	2.91	2.45	2.08	1.76

channelized (97.7 ± 2.06 SE) reaches. PCA axes 1 and 2 explain 89.4% of the variation in individual habitat-quality metrics among sites, and 73.1% was explained by axis 1 alone (Table 6). Scores on PCA axis 1 and 2 indicate that variation in habitat quality was greater among unchannelized than channelized sites—as indicated by larger distances separating unchannelized sites on these two axes (Figure 5). The unchannelized sites 2 and 3 were most strongly differentiated from the channelized sites along axis 1, and unchannelized site 1 was differentiated from all other sites along axis 2 (Figure 5). Epifaunal substrate/available cover was most strongly (and positively) correlated with axis 1—indicated by a small vector angle—but scores were less variable in magnitude than those for sediment deposition, channel alteration, and channel sinuosity—indicated by shorter vector length. Higher scores on axis 1 for channel sinuosity and pool substrate characterization were negatively correlated with those for bank stability—as indicated by vectors in the opposite direction—and differentiated site 3 from other sites (lower right in Figure 5). Channelized sites 4, 5, and 6 were differentiated from unchannelized sites 2 and 3 along axis 1 by higher scores for channel flow status, and from unchannelized site 1 along axis 2 by lower scores for most other variables (lower left of Figure 5). Table 7 shows site scores for each individual metric.

Fish Assemblage Structure

Seines were most effective at capturing small-bodied cyprinids and mosquitofish, and the most effective gear for sampling invertivore biomass, but not omnivore and piscivore biomass. Electrofishers were effective for sampling centrarchid biomass in

TABLE 6.? Summary data from the principal components analysis (PCA) of sites based on habitat quality assessment metrics. Eigenvalues, proportions of variation, and cumulative proportions are given for each of the first four principal components.

	Axis	Site Biomass
Eigenvalues	1	0.731
	2	0.162
	3	0.065
	4	0.033
% variance	1	73.1
	2	16.3
	3	6.5
	4	3.3
Cumulative % variance	1	73.1
	2	89.4
	3	95.9
	4	99.2
Total Inertia	Sum of all	1.000

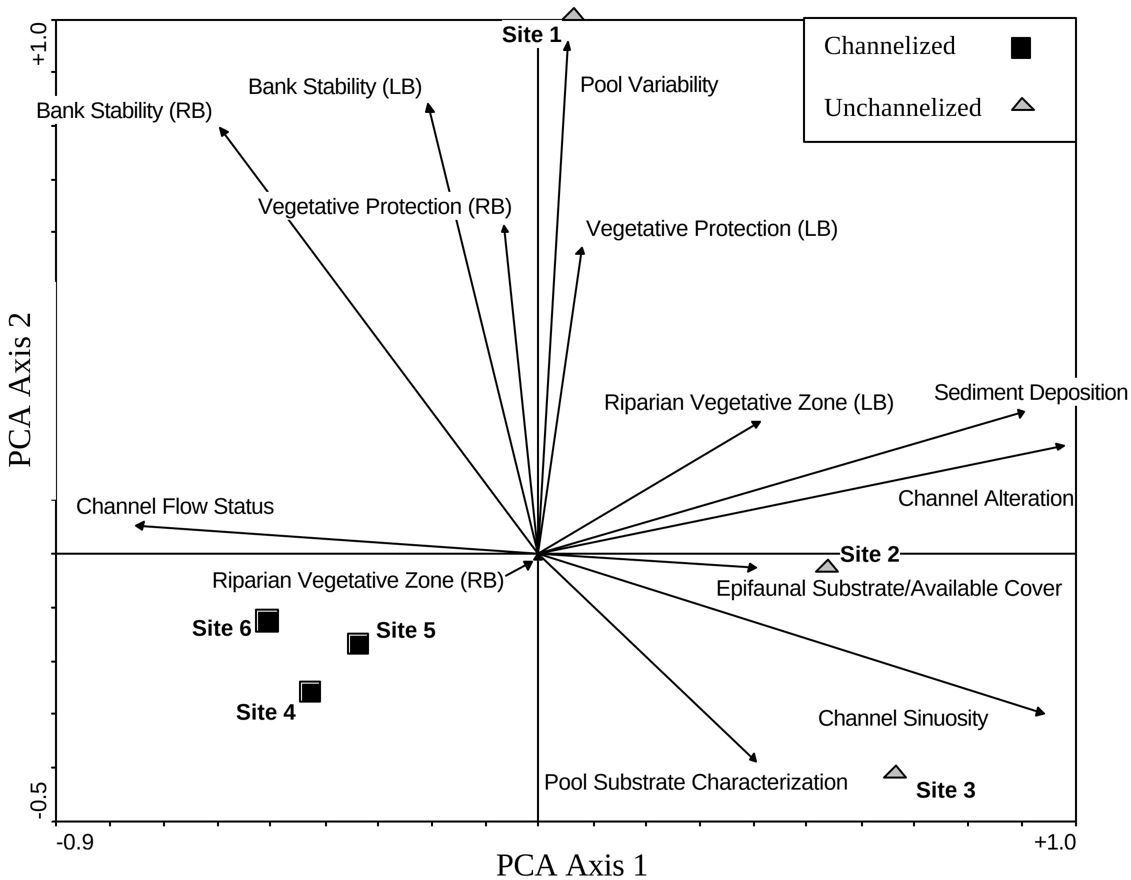

FIGURE 5.? Plot of principal components analysis (PCA) of sites and habitat quality metrics. Centroids indicate sites. Vectors point in the direction of the maximum variation in the site values. Length of the vector is proportional to the maximum rate of change. A smaller angle between the axis and vector indicates a stronger correlation.

TABLE 7.? Scores for individual habitat quality metrics (Table 2) and totals for each site.

		Site #					
		Unchannelized			Channelized		
Habitat Quality Assessment Metric		1	2	3	4	5	6
1	Epifaunal Substrate/Available Cover	7	6	8	8	6	4
2	Pool Substrate Characterization	6	8	8	7	5	8
3	Pool Variability	12	6	5	4	5	7
4	Sediment Deposition	14	15	15	8	11	6
5	Channel Flow Status	14	11	12	13	15	19
6	Channel Alteration	15	19	19	5	6	5
7	Channel Sinuosity	6	14	18	4	5	5
8	Bank Stability						
	Left Bank	9	5	5	6	7	5
	Right Bank	9	4	2	6	6	6
9	Vegetative Protection						
	Left Bank	9	8	8	7	9	8
	Right Bank	9	7	5	7	3	8
10	Riparian Vegetative Zone						
	Left Bank	10	10	10	9	10	10
	Right Bank	10	10	10	10	10	10
	TOTAL SCORE	130	123	125	94	98	101

TABLE 8.—Common and scientific names, species codes in multivariate analyses, trophic group, and tolerance of all species collected. Trophic group abbreviations are: P = piscivore, IF = invertivore, O = omnivore.

Common Name	Scientific Name	Code	Trophic Group	Tolerant/Intolerant
Spotted Gar	*Lepisosteus occulatus*	LOCC	P	T
Longnose Gar	*Lepisosteus osseus*	LOSS	P	T
Shortnose Gar	*Lepisosteus platostomus*	LPLA	P	T
Gizzard Shad	*Dorosoma cepedianum*	DCEP	O	T
Red Shiner	*Cyprinella lutrensis*	CLUT	IF	T
Common Carp	*Cyprinus carpio*	CARP	O	T
Mississippi Silvery Minnow	*Hybognathus nuchalis*	HNUC	O	T
Ribbon Shiner	*Lythrurus fumeus*	LFUM	IF	-
Redfin Shiner	*Lythrurus umbratilis*	LUMB	IF	-
Emerald Shiner	*Notropis atherinoides*	NATH	IF	-
Ghost Shiner	*Notropis buchanani*	NBUC	IF	-
Mimic Shiner	*Notropis volucellus*	NVOL	IF	I
Bullhead Minnow	*Pimephales vigilax*	PVIG	IF	-
River Carpsucker	*Carpoides carpio*	CCAR	O	T
Smallmouth Buffalo	*Ictiobus bubalus*	IBUB	O	-
Bigmouth Buffalo	*Ictiobus cyprinellus*	ICYP	IF	T
Blue Catfish	*Ictalurus furcatus*	IFUR	P	-
Channel Catfish	*Ictalurus punctatus*	IPUN	O	T
Tadpole Madtom	*Noturus gyrinus*	NGYR	IF	I
Freckled Madtom	*Noturus nocturnus*	NNOC	IF	I
Flathead Catfish	*Pylodictis olivaris*	POLI	P	-
Pirate Perch	*Aphredoderus sayanus*	ASAY	IF	-
Blackstripe Topminnow	*Fundulus notatus*	FNOT	IF	-
Western Mosquitofish	*Gambusia affinis*	GAFF	IF	T
Inland Silverside	*Menidia beryllina*	MBER	IF	-
Green Sunfish	*Lepomis cyanellus*	LCYA	P	T
Warmouth	*Lepomis gulosus*	LGUL	P	T
Orangespotted Sunfish	*Lepomis humilis*	LHUM	IF	-
Bluegill	*Lepomis macrochirus*	LMAC	IF	T
Dollar Sunfish	*Lepomis marginatus*	LMAR	IF	-
Longear Sunfish	*Lepomis megalotis*	LMEG	IF	-
Sunfish < 20mm	*Lepomis* spp.	LSPP	IF	-
Largemouth Bass	*Micropterus salmoides*	MSAL	P	-
White Crappie	*Pomoxis annularis*	PANN	P	-
Slough Darter	*Etheostoma gracile*	EGRA	IF	-
Freshwater Drum	*Aplodinotus grunniens*	AGRU	IF	T

TABLE 9.? Common species (>1% of the total catch for a particular gear type) included in all multivariate analyses.

Gear Type	Common Name	Scientific Name
Gill Net	Longnose Gar	*Lepisosteus osseus*
	Shortnose Gar	*Lepisosteus platostomus*
	Gizzard Shad	*Dorosoma cepedianum*
	Common Carp	*Cyprinus carpio*
	River Carpsucker	*Carpoides carpio*
	Smallmouth Buffalo	*Ictiobus bubalus*
	Bigmouth Buffalo	*Ictiobus cyprinellus*
	Channel Catfish	*Ictalurus punctatus*
	Flathead Catfish	*Pylodictis olivaris*
	White Crappie	*Pomoxis annularis*
Seine	Red Shiner	*Cyprinella lutrensis*
	Redfin Shiner	*Lythrurus umbratilis*
	Mimic Shiner	*Notropis volucellus*
	Bullhead Minnow	*Pimephales vigilax*
	Western Mosquitofish	*Gambusia affinis*
	Bluegill	*Lepomis macrochirus*
	Sunfish < 20mm	*Lepomis* spp.
Electrofisher	Red Shiner	*Cyprinella lutrensis*
	Redfin Shiner	*Lythrurus umbratilis*
	Bullhead Minnow	*Pimephales vigilax*
	Western Mosquitofish	*Gambusia affinis*
	Green Sunfish	*Lepomis cyanellus*
	Orangespotted Sunfish	*Lepomis humilis*
	Bluegill	*Lepomis macrochirus*
	Longear Sunfish	*Lepomis megalotis*
	Sunfish < 20mm	*Lepomis* spp.
	Freckled Madtom	*Noturus nocturnus*
	Slough Darter	*Etheostoma gracile*

complex structural habitats, such as undercut banks, tree roots, and woody debris, and contributed to samples of piscivore and invertivore biomass, but not omnivores. Seines and electrofishers captured fishes in all mesohabitat types, however seines captured schooling fishes (small cyprinids and juvenile sunfishes) in open water, and electrofishers captured fishes associated with complex habitat structure. Gill nets captured 10 out of the 21 common species. Gill nets also captured more of the large-bodied piscivores and were the only gear that captured omnivores, which in this river system comprised most of the large-bodied species. Gill nets were only deployed in pool mesohabitats and, therefore, only represented species captured in pools.

A total of 6,799 fish representing 35 species was collected during the study (Table 8). Of these, 31 species were collected in both reaches. Warmouth, ghost shiner, tadpole madtom, and shortnose gar were collected only in channelized areas. However, of those species, only shortnose gar were considered common (i.e., >1% of the total catch) and included in multivariate analyses (Table 9). For total fish density summed across all gears and collections (Figure 6), red shiner was most abundant (23.7%), followed by smallmouth buffalo (16.9%), bullhead minnows (12.1%), and western mosquitofish (8.2%). For total fish density by gear type summed across collections (Figure 7), gill nets caught proportionally more large-bodied species. It was the only gear that caught fishes in the families Lepisosteidae (longnose gar and shortnose gar), Clupeidae (gizzard shad), and catastomidae (river carpsucker, smallmouth buffalo, and bigmouth buffalo), and the only gear that caught common carp (a large cyprinid), channel catfish and flathead catfish (large ictalurids), and white crappie (a large

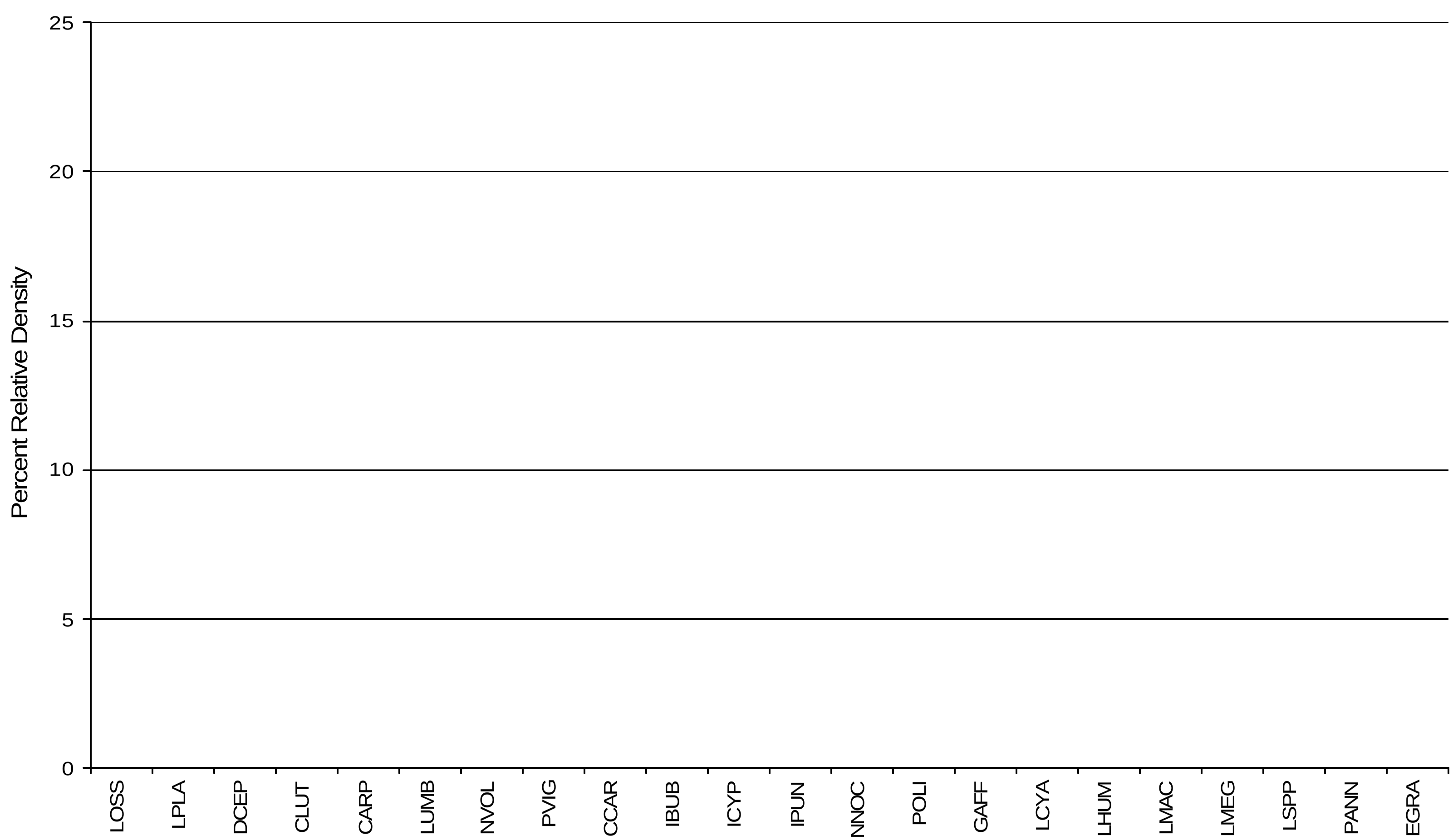

FIGURE 6.? Percent of relative density of the total catch for each species when all gear types are combined.

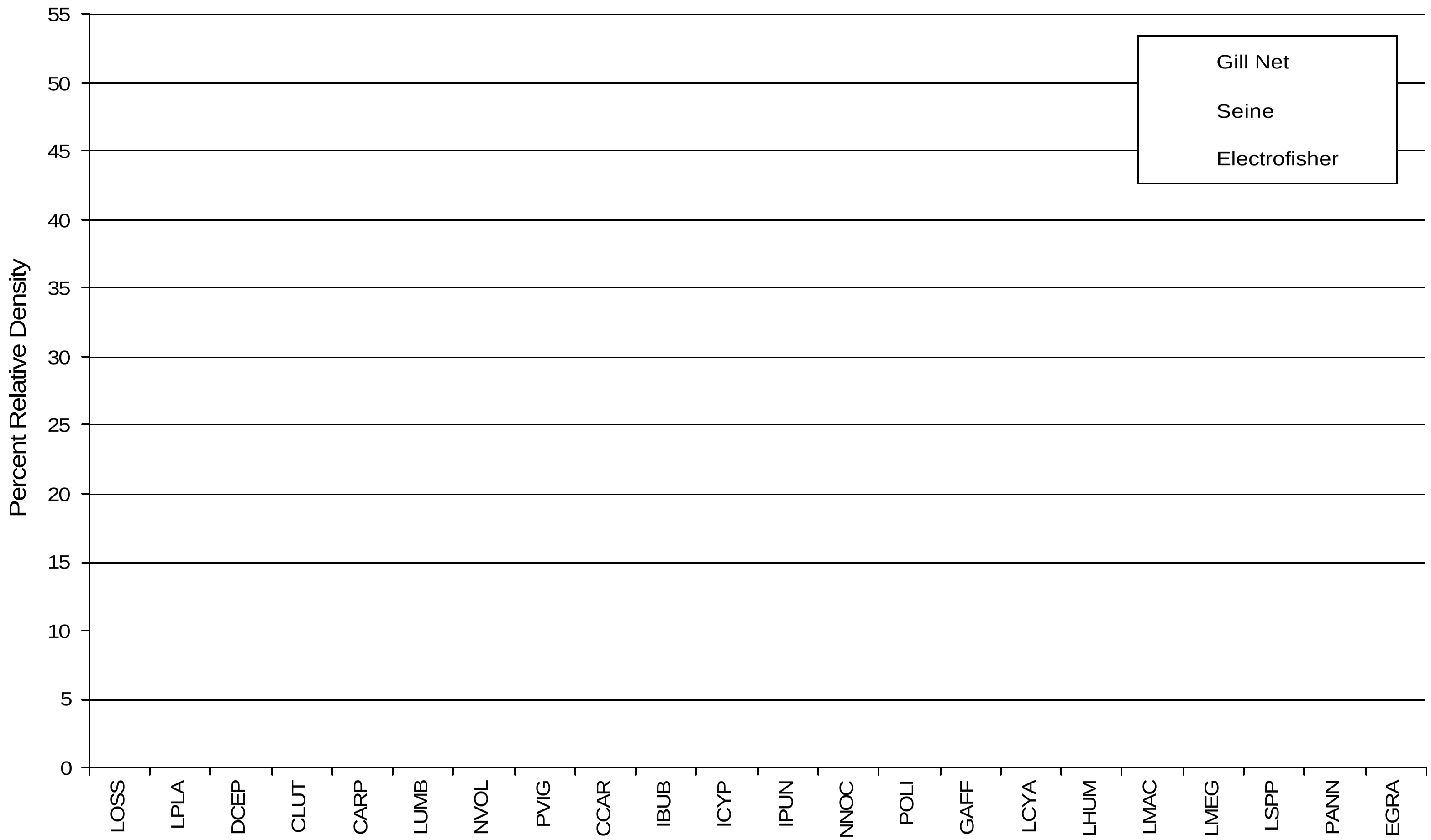

FIGURE 7.? Percent of relative density of the total catch for each species within a particular gear type.

centrarchid). Seines and electrofishing captured primarily small cyprinids and western mosquitofish, but electrofishing also caught a greater proportion of centrarchids and freckled madtom (Figure 7).

Univariate Analyses

There was no significant year or year-by-reach interaction for any of the univariate analyses. Species richness did not differ between reaches; 18.0 species (± 0.62 SE) were captured in the unchannelized reach and 18.8 (± 0.62 SE) in the channelized reach. As expected, sites in the unchannelized reach contained a greater mean proportion (13.0 % ± 0.02 SE) of the total fish density across both years than did sites in the channelized reach (3.6 % ± 0.02 SE). On average 39.1% of the total catch was caught in the unchannelized reach and 10.9% in the channelized reach. Number of tolerant species was higher in the channelized (8.8 ± 0.17 SE) than unchannelized (8.2 ± 0.17 SE) reach. Overall scores of the IBI were similar for the unchannelized (44.7 ± 1.05 SE) and channelized (45.3 ± 1.05 SE) reaches. Both reaches indicated an overall aquatic life use rating of “high” (Table 3).

Multivariate Analyses

Eigenvalues from the ordination axes indicate the maximized dispersion of the species scores, and is thus a measure of the importance of the axes. Values over 0.5 often denote a good separation of the species along the axis, and therefore display biologically relevant information (Jongman et al. 1995). Eigenvalues were greater than

0.5 on the first two axes, and generally less than 0.5 on axes 3 and 4. Therefore, only the results for the first two axes are displayed on ordination plots.

CA of Mesohabitat Level x Species Density.—Axes 1 and 2 explained 18.6% and 15.1% of the variation in distribution of species' abundances (Table 10). Axis 1 (Figure 8) indicates a gradient of mesohabitat types from pools (toward the upper left) to riffles (toward the lower right), and separates species associated with channelized (toward the left) and unchannelized sites (toward the right). The exception to this pattern was a cluster of three unchannelized pools (upper left of Figure 8) in 2001. Axis 2 indicates a general trend from summer 2001 to summer 2002 (top to bottom in Figure 8).

Gill nets were only deployed in pools, and more individuals were caught in gill nets in 2001 than 2002. The cluster of pool samples for unchannelized sites in 2001—plotted near pool samples for channelized sites—was associated with species captured in higher abundances in gill nets. Therefore, in 2002, pool samples in unchannelized sites were dominated by species captured by seining and electrofishing. Species associated with channelized pools included common carp, flathead catfish, smallmouth buffalo, longnose gar, and orangespotted sunfish. Species associated with unchannelized pools included unidentified juvenile sunfishes (*Lepomis* spp.), western mosquitofish, and longear sunfish. The only backwater habitat across all sites occurred at site three in the unchannelized reach, and was associated with bluegill in 2001, but with red shiner in 2002 (Figure 8). Species dominating runs were red shiner, mimic shiner, and redfin shiner captured by electrofishing—redfin shiner in seine samples was associated with deeper and more sluggish pool or backwater habitats. Riffle habitats were associated

TABLE 10.? Summary of correspondence analyses (CA) of relative abundance of total fish densities and densities of juvenile or adult life stages by sites and mesohabitat types.

	Axis	Mesohabitats x Species	Mesohabitats x Juv or Adult	Sites x Species	Sites x Juv or Adult
Eigenvalues	1	0.683	0.691	0.494	0.534
	2	0.554	0.571	0.444	0.480
	3	0.460	0.513	0.298	0.338
	4	0.361	0.392	0.260	0.279
% variance	1	18.6	16.2	26.6	25.4
	2	15.1	13.5	23.9	22.7
	3	12.6	12.0	16.0	16.1
	4	9.8	9.3	14.5	13.2
Cumulative % variance	1	18.6	16.2	26.6	25.4
	2	33.7	29.7	50.5	48.1
	3	46.3	41.7	66.5	64.2
	4	56.1	51.0	80.5	77.4
Total Inertia	Sum of all	3.667	4.253	1.858	2.105

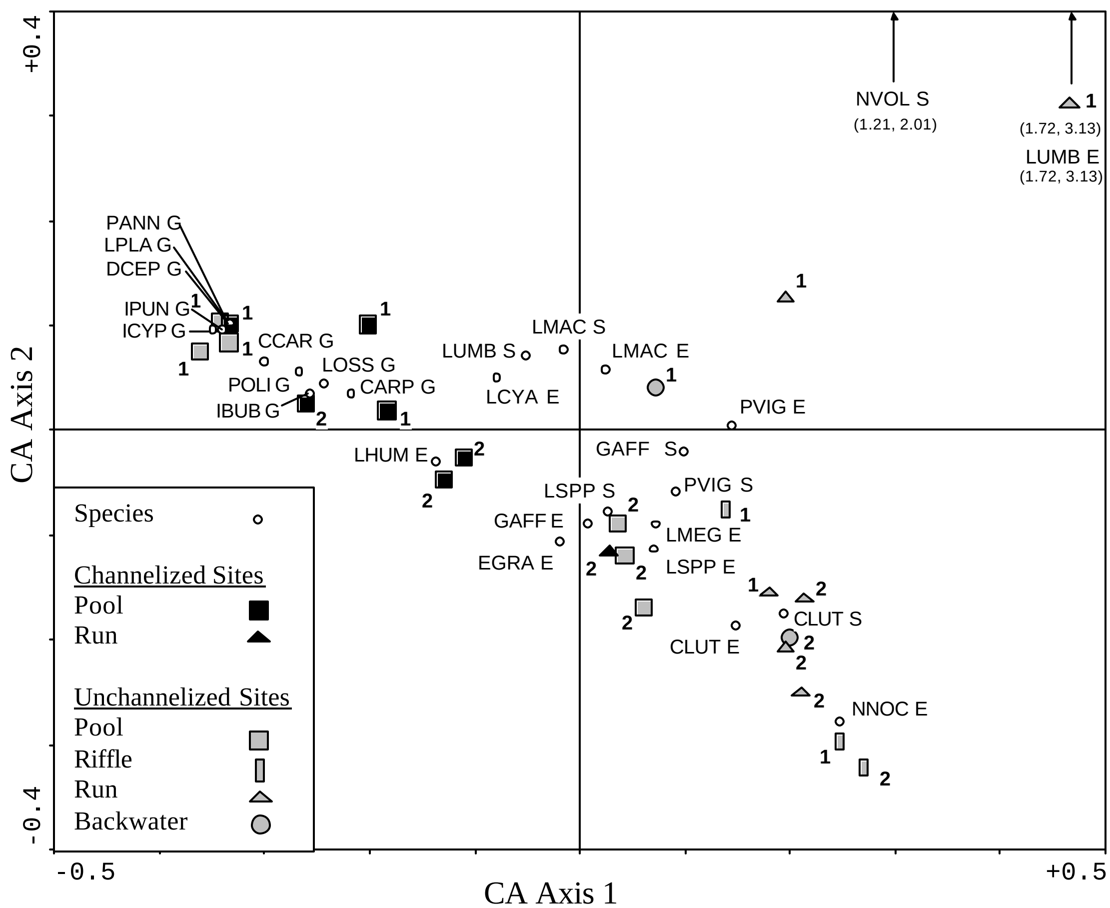

FIGURE 8.? Results of correspondence analysis (CA) for species abundance across mesohabitats within each reach.

with freckled madtom.

CA of Mesohabitat Level x Juvenile and Adult Species Density.—Axes 1 and 2 explained 16.2% and 13.5% of the spatial variation in species abundance (Table 10), which is similar to that for the previous CA. Overall, distributions of both juvenile and adult stages of a particular species were similar to distribution patterns across mesohabitats for species' densities shown in the previous CA, with a few exceptions. Juvenile slough darters were associated with pools in both channelized and unchannelized reaches (as in the previous CA for both life stages combined), whereas adults were more affiliated with run mesohabitat in the unchannelized reach. Similarly, juvenile green sunfish remained associated with pools in the channelized reach and backwaters in the unchannelized reach, whereas adults were more associated with pools in the channelized reach (Figure 9).

CA of Site Level x Species Density.—Axis 1 and 2 account for 26.6% and 23.9% of the variance in spatial species distribution (Table 10). Axis 1 separates collections by reach, with channelized on the right and unchannelized on the left (Figure 10). Axis 2 more strongly separates collections by year for the unchannelized than channelized reach. Thus, differences among assemblages within and between reaches were greater in 2001 than 2002. In 2001, sites in the channelized reach (far right in Figure 10) were most strongly associated with species in gill netted samples and included gizzard shad, white crappie, shortnose gar, longnose gar, and river carpsucker, whereas sites in the unchannelized reach (upper left in Figure 10) were associated with species captured by multiple gears, including redfin shiner, mimic shiner, channel catfish, bluegill, and

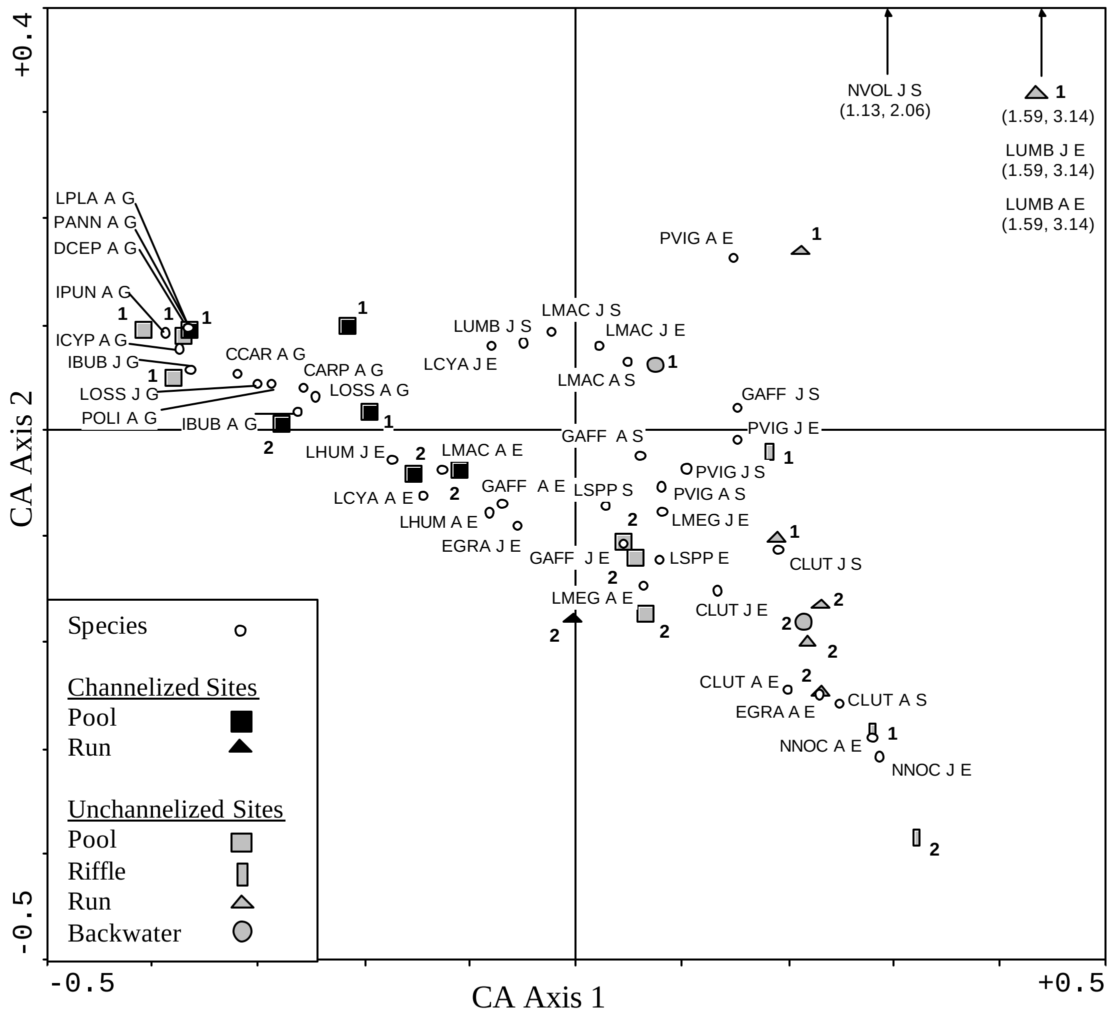

FIGURE 9.? Plot of correspondence analysis (CA) using species scaling revealing the relationships between species abundance of juvenile and adult life stages and mesohabitats within each reach.

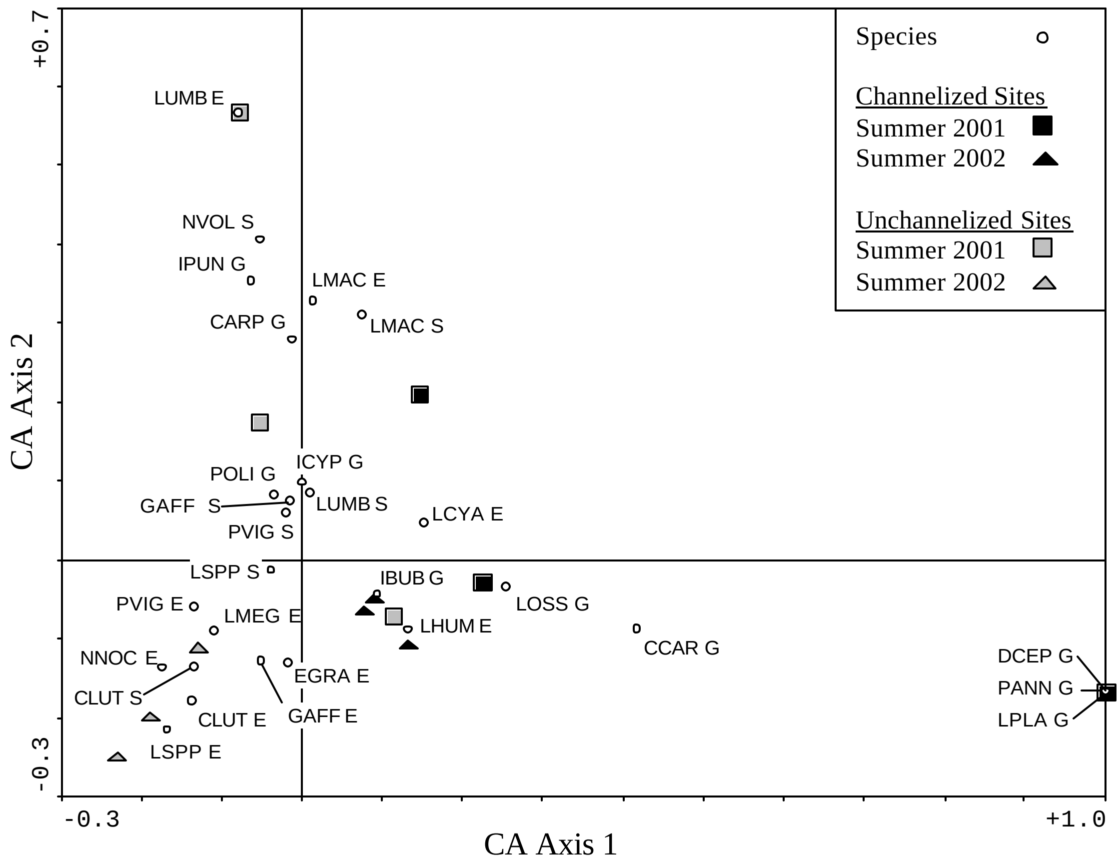

FIGURE 10.? Plot of correspondence analysis (CA) using species scaling revealing the relationships between total species abundance and sites within each reach.

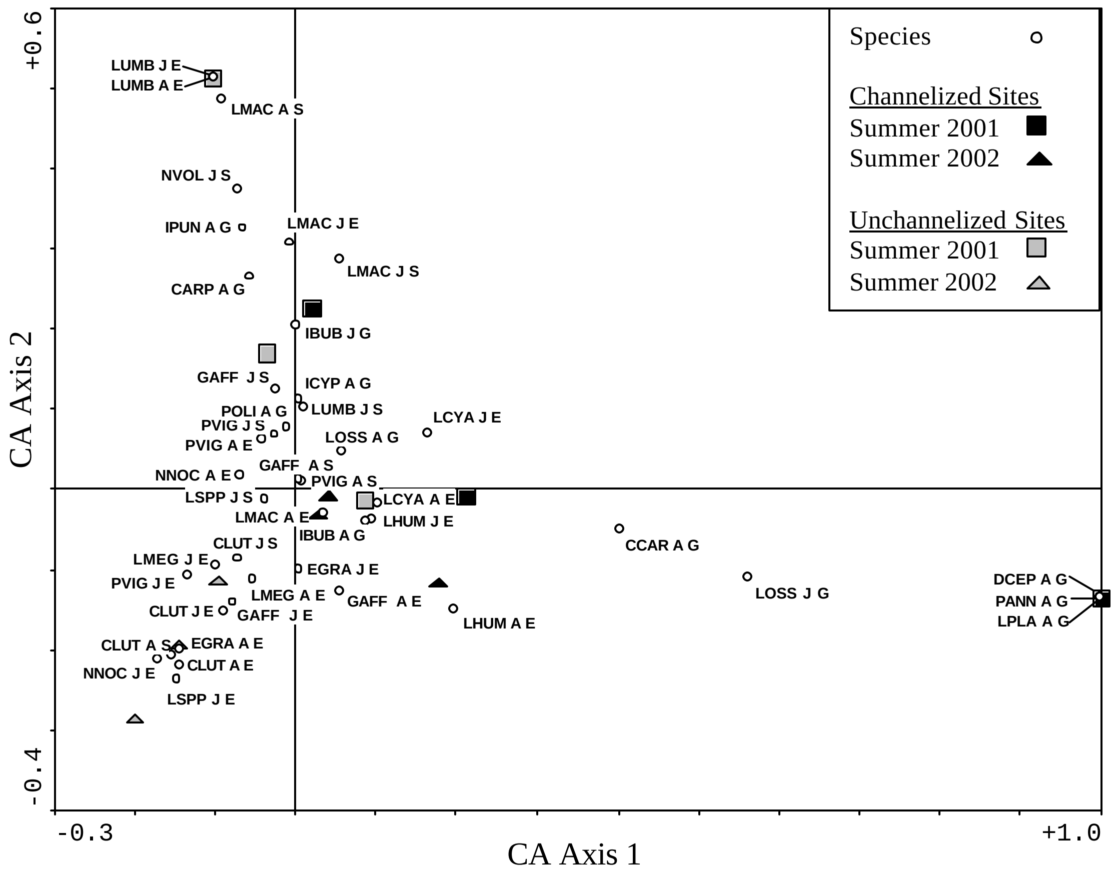

FIGURE 11.? Plot of correspondence analysis (CA) using species scaling revealing the relationships between species abundance of juvenile and adult life stages and sites within each reach.

common carp. In 2002, sites in the channelized reach (center of Figure 10) were associated with smallmouth buffalo and orangespotted sunfish, and sites in the unchannelized reach (lower left in Figure 10) were associated with red shiner, freckled madtom, longear sunfish, as well as unidentified juvenile sunfish, bullhead minnow, and western mosquitofish.

CA of Site Level x Juvenile and Adult Species Density.—Axis 1 and 2 of the CA explained 25.4% and 22.7% of the variation in species abundance and distribution (Table 10) and similar to that for the CA of species density. Again, the CA for separation of life stages into juveniles and adults is very similar to the CA for species density with a few exceptions. Adult bluegill were more associated with sites in the unchannelized reach in 2001, whereas in 2002 they were not strongly associated with either reach (Figure 11). Juvenile longnose gar were strongly associated with channelized sites, whereas adults were not strongly associated with either reach. Adult orangespotted sunfish were primarily captured in 2002 and were associated with channelized sites, whereas juveniles were not strongly associated with either reach. The association of smallmouth buffalo with channelized sites was primarily due to adults in both years, whereas in 2001 juveniles were associated with both reaches. Adult slough darters were more associated with unchannelized sites than were juveniles.

CA of Site Level x Species Biomass.—A CA was done on relative biomass to determine the trophic structure of each reach. Axis 1 and 2 explained 25.4% and 22.4% of the variation in species distribution (Table 11). Sites in the channelized reach included species with higher biomass attributed to piscivores and omnivores (Figure 12).

TABLE 11.? Summary of correspondence analysis based on percent biomass of sites. Summary of a correspondence analysis (CA) revealing the trophic relationships between the relative biomass of species and sites within each reach.

	Axis	Site Biomass
Eigenvalues	1	0.525
	2	0.462
	3	0.425
	4	0.294
% variance	1	25.4
	2	22.4
	3	20.6
	4	14.3
Cumulative % variance	1	25.4
	2	47.8
	3	68.4
	4	82.7
Total Inertia	Sum of all	2.064

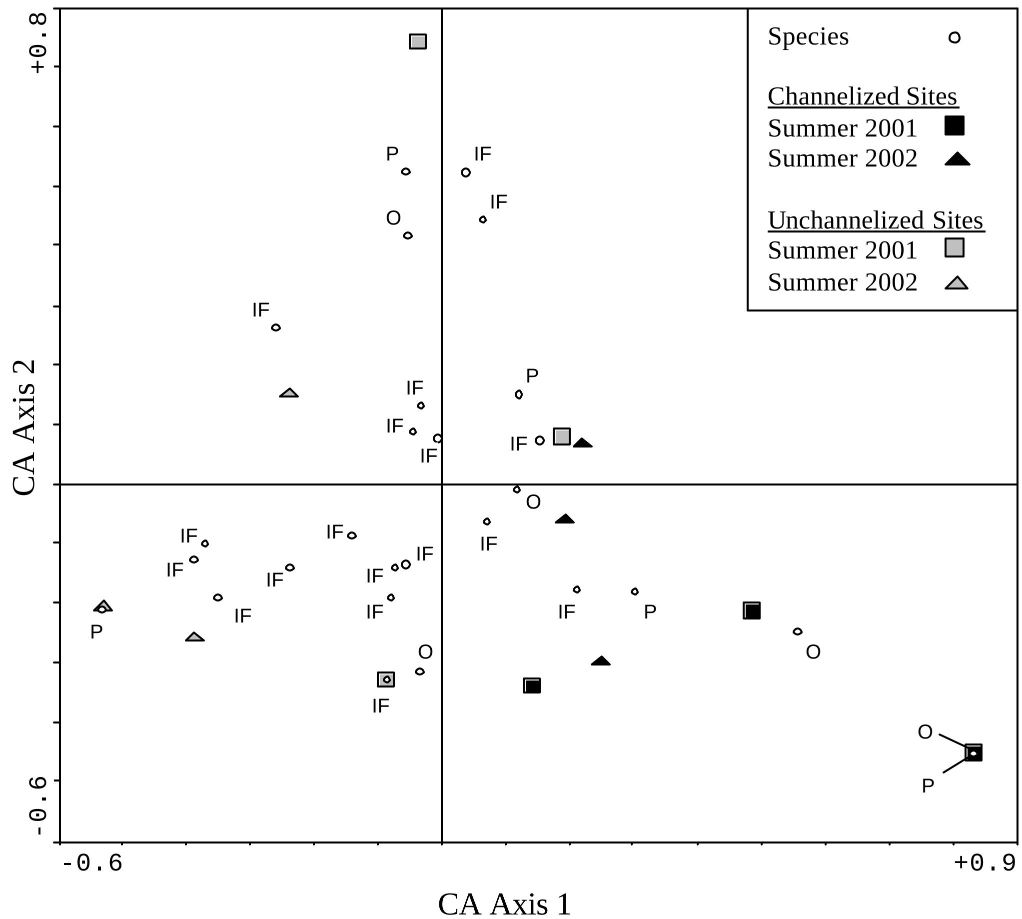

FIGURE 12.? Plot of correspondence analysis (CA) revealing the trophic relationships between the relative biomass of species (species centroids displayed as trophic groups) and sites within each reach. P = Piscivore, IF = Invertivore, and O = Omnivore.

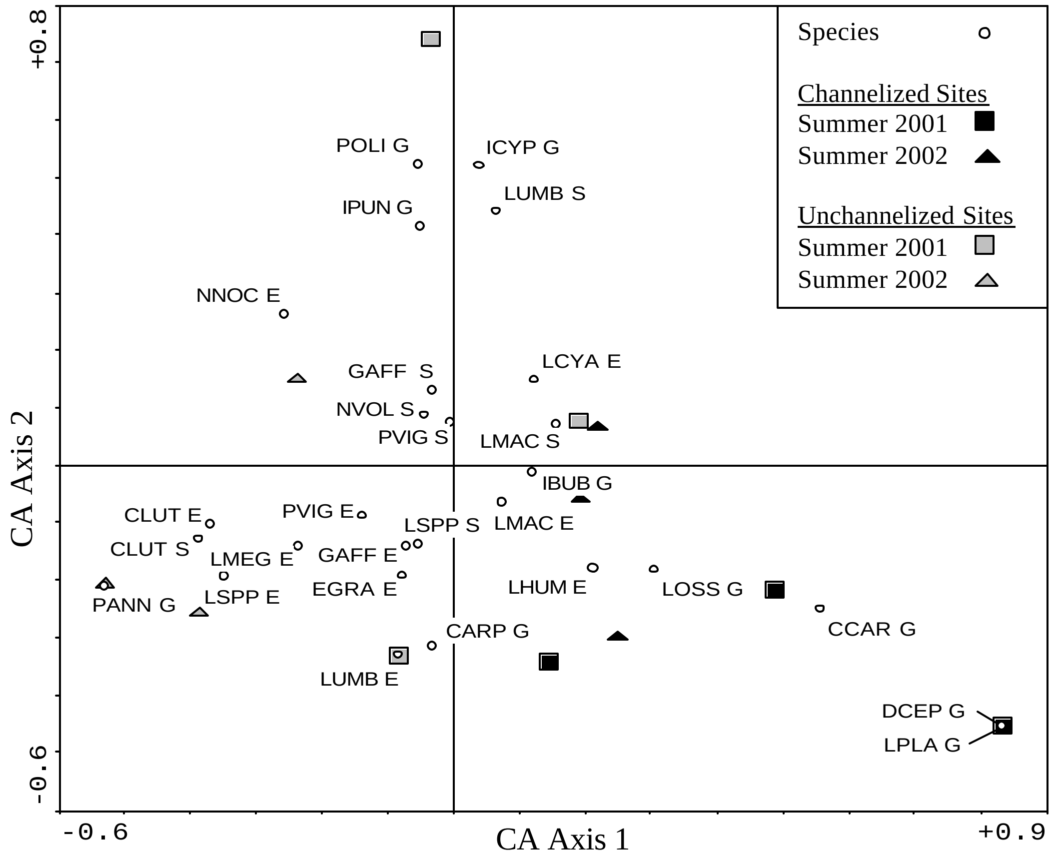

FIGURE 13.? Plot of correspondence analysis (CA) revealing the trophic relationships between the relative biomass of species and sites within each reach. Species designations of each centroid are displayed.

The unchannelized reach was associated with more species and higher biomass of invertivores as compared to the channelized reach (Figure 12). Species associated with the channelized reach included piscivorous longnose and shortnose gar, and omnivorous gizzard shad and river carpsucker. Orangespotted sunfish was the only invertivorous species associated with the channelized reach (Figure 13). Cyprinids (redfin shiner, red shiner, mimic shiner, and bullhead minnow) were associated with the unchannelized reach (Figure 13), along with four other invertivores—freckled madtom, longear sunfish, bigmouth buffalo, and western mosquitofish. Two piscivores—flathead catfish and white crappie—and one omnivore—channel catfish were also associated with the unchannelized reach. There were no herbivorous species collected in either reach, likely due to lack of algae and absence of submerged vegetation.

MANOVAR.—Percentage of biomass differed across trophic groups, but differently depending on reach (Figure 14). Effects of year and reach independently on trophic biomass were not statistically significant. Across both years and both reaches, omnivores comprised the highest proportional biomass (50%), followed by invertivores (30%), and piscivores (20%). However, there was a significant trophic group by reach interaction. The proportional biomass of piscivores was higher in the channelized reach, but for both invertivores and omnivores, it was higher in the unchannelized reach (Figure 14).

CCA.—The variable pool was excluded from the CCA because it had negligible variance, whereas run and habitat quality scores were excluded because they were collinear to the remaining variables (variance inflation scores > 6), causing erroneous

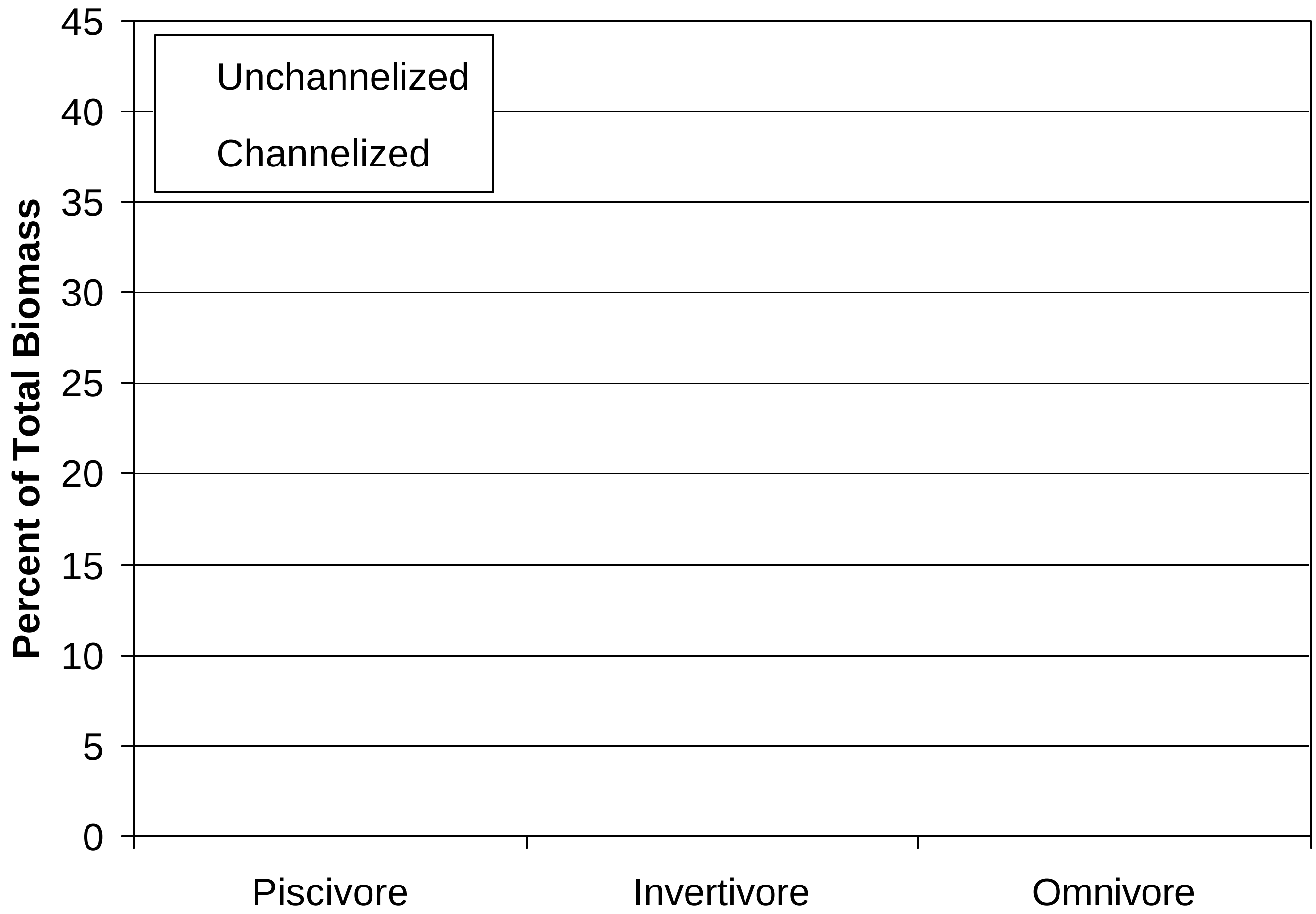

FIGURE 14.? Percent of the total biomass collected in both the unchannelized and channelized reach across 2001 and 2002.

correlation coefficients due to overfitting the model. The remaining environmental variables had variance inflation scores < 2, and explained 38.9% of the total species variation. The first two canonical axes explained 34.2% of the variation in species composition and 87.8% of the species-environment relationship (Table 12). The partial CCA determined that reach variables (channelized and unchannelized) independently explained 10.7% of the species variation, and the remaining mesohabitat variables (riffle and backwater) independently explained 23.4%. Thus, 34.1% of the species variation was explained independently by these variables, with the remaining 4.8% shared between reach and mesohabitat variables. Monte Carlo tests showed that both axis 1 and all axes together each explained significant variation in species distribution and abundance (Table 12). A partial CCA determined that reach was a significant predictor of the variation in species abundance, even after accounting for mesohabitat type (Table 12).

All explanatory variables are categorical and therefore plotted as centroids that indicate the center of sample dispersion for each variable (Figure 15). Species are plotted as centroids that indicate their association with explanatory variables in the analysis. Species centroids closer to explanatory variables indicate stronger correlation of species densities with those variables (Jongman et al. 1995).

CCA axis 1 represents a gradient from channelized to unchannelized reaches (left to right in Figure 15), and axis 2 represents a gradient of mesohabitats from backwater to riffle (top to bottom in Figure 15). The centroid for the environmental variable channelized reach, and centroids for all sites in that reach, are located in the upper left

TABLE 12.? Summary of canonical correspondence analysis based on species relative density and environmental variables. Summary of partial canonical correspondence analyses show partitioning of variance in species distribution accounted for by each component of interest.

		All variables	Partial variables	
	Axis	Reach + Mesohabitat	Reach	Mesohabitat
Eigenvalues	1	0.367	0.198	0.318
	2	0.268	0.367	0.117
	3	0.088	0.330	0.367
	4	0.367	0.177	0.330
Species-environment correlations	1	0.931	0.782	0.896
	2	0.826	0.000	0.856
	3	0.791	0.000	0.000
	4	0.000	0.000	0.000
Cumulative % variance of species data	1	19.8	14.9	20.2
	2	34.2	42.4	27.7
	3	38.9	67.1	51.1
	4	58.7	80.4	72.1
Cumulative % of variance of species-environment relation	1	50.8	100.0	73.0
	2	87.8	0.00	100.0
	3	100.0	0.00	0.0
	4	0.0	0.00	0.0
Unconstrained eigenvalues	Sum of all	1.858	1.333	1.570
Canonical eigenvalues	1-3	0.723	0.198	0.435
P-value	1	0.0300	0.0150	0.0200
	1-3	0.0050	0.0150	0.0050
% variance explained	1-3	38.9	10.7	23.4

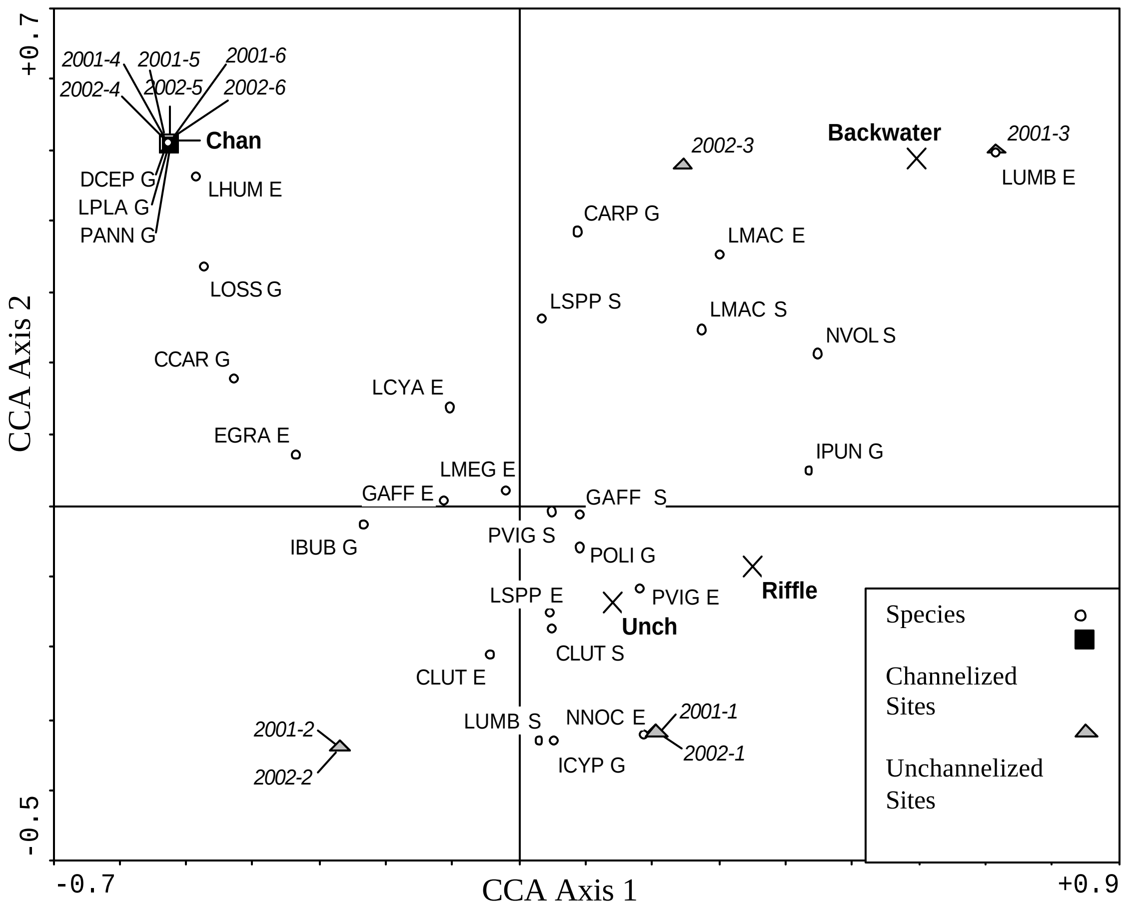

FIGURE 15.? Plot of canonical correspondence analysis (CCA) using species scaling revealing the relationships between total species abundance, sites within each reach, and categorical explanatory variables plotted as centroids.

quadrant (Figure 15), likely because these sites contained predominantly pool habitat, which has similar characteristics for water velocity to those of backwaters. Species associated with the channelized reach were gizzard shad, shortnose gar, white crappie, orangespotted sunfish, longnose gar, and river carpsucker. Species associated with the unchannelized reach were bullhead minnow, flathead catfish, freckled madtom, red shiner, longear sunfish, western mosquitofish, bigmouth buffalo, unidentified juvenile sunfish, redfin shiner, and mimic shiner. Species associated with backwater habitats were bluegill and redfin shiner collected by electrofishing, whereas species associated with riffles included bullhead minnow, freckled madtom, and red shiner.

ISA of Mesohabitat Level x Species Density.—Among the four mesohabitat types, pool and riffle each had one indicator species, run had none, and backwater had two indicator species (Table 13). The significant indicator of pool habitat was smallmouth buffalo (caught only in gill nets) and riffle habitat was indicated by freckled madtom. Bluegill and unidentified juvenile sunfish (captured by seining) were indicators of backwaters.

ISA of Mesohabitat Level x Juvenile and Adult Species Density.—Juveniles and adults that were significant mesohabitat indicators in this ISA were the same species and mesohabitat indicators as those in the ISA of species density (Table 14). However, two species showing high (but nonsignificant) values indicated trends in mesohabitat segregation by life-history stage. Red shiner adults had higher indicator values for riffles, whereas juveniles had higher indicator values for runs; slough darter adults had higher indicator values for runs, whereas juveniles had higher indicator values for pools (Table 14).

ISA of Reach x Species Density.—The unchannelized reach had four indicator species, but the channelized reach had only one significant indicator species (Table 15). Red shiners, bullhead minnows, western mosquitofish, and longear sunfish were indicators of the unchannelized reach; orangespotted sunfish was the indicator of the channelized reach.

ISA of Reach x Juvenile and Adult Species Density.—As for the mesohabitat level ISA, juveniles and adults that were significant indicators in this ISA were the same species and reach indicators in the ISA of species density (Table 16). As previously noted for mesohabitats, two species showed high (but nonsignificant) values that indicated trends for segregation of life-history stages by reach. Slough darter adults had higher indicator values for the unchannelized reach, whereas juveniles had higher indicator values for the channelized reach; green sunfish adults had higher indicator values for the channelized reach, whereas juveniles had higher indicator values for the unchannelized reach (Table 16).

TABLE 13.? Indicator values for fishes based on their relative abundance and frequency of occurrence in mesohabitat types of the South Sulphur River. Proportions of Monte Carlo randomized trials (1000) having indicator value equal to or exceeding those observed is given for each species. Bold font designates highest indicator value for each species and species that are significant indicators of a particular mesohabitat type.

		Mesohabitat			
Species	P	Pool	Riffle	Run	Backwater
IBUB G	**0.000**	**100**	0	0	0
LOSS G	0.056	**50**	0	0	0
LHUM E	0.146	**44**	0	2	0
LCYA E	0.392	**38**	3	33	0
GAFF E	0.381	**38**	1	18	10
EGRA E	0.385	**33**	0	7	0
CARP G	0.235	**33**	0	0	0
LSPP E	0.637	**25**	0	21	0
CCAR G	0.339	**25**	0	0	0
POLI G	0.457	**25**	0	0	0
ICYP G	0.674	**17**	0	0	0
IPUN G	0.687	**17**	0	0	0
DCEP G	0.999	**8**	0	0	0
LPLA G	0.999	**8**	0	0	0
PANN G	0.999	**8**	0	0	0
NNOC E	**0.038**	0	**59**	3	0
CLUT S	0.503	6	**39**	25	2
CLUT E	0.613	9	**32**	26	1
LMEG E	0.378	28	3	**38**	3
GAFF S	0.694	13	25	**35**	21
PVIG E	0.718	16	1	**34**	20
PVIG S	0.923	11	24	**28**	25
NVOL S	0.287	0	0	**27**	0
LUMB E	0.513	0	0	**14**	0
LUMB S	0.973	5	**7**	**7**	0
LMAC E	**0.012**	8	0	5	**83**
LSPP S	**0.001**	16	0	4	**69**
LMAC S	0.276	5	0	4	**41**

TABLE 14.? Indicator values for juvenile and adult fishes based on their relative abundance and frequency of occurrence in mesohabitat types of the South Sulphur River. Proportions of Monte Carlo randomized trials (1000) having indicator value equal to or exceeding those observed is given for each species. Bold font designates highest indicator value for each species and species that are significant indicators of a particular mesohabitat type.

		Mesohabitat			
Species	P	Pool	Riffle	Run	Backwater
IBUB A G	**0.000**	**92**	0	0	0
GAFF A E	0.122	**50**	0	14	0
LOSS A G	0.121	**42**	0	0	0
LHUM J E	0.147	**42**	0	0	0
EGRA J E	0.213	**40**	0	6	0
LCYA J E	0.404	**38**	4	25	0
LCYA A E	0.437	**35**	0	8	0
CARP A G	0.245	**33**	0	0	0
GAFF J E	0.808	**25**	2	18	13
LSPP J E	0.666	**25**	0	21	0
LHUM A E	0.971	**13**	0	7	0
CCAR A G	0.377	**25**	0	0	0
IBUB J G	0.378	**25**	0	0	0
LOSS J G	0.438	**25**	0	0	0
POLI A G	0.488	**25**	0	0	0
ICYP A G	0.709	**17**	0	0	0
IPUN A G	0.709	**17**	0	0	0
LMAC A E	0.709	**17**	0	0	0
DCEP A G	0.999	**8**	0	0	0
LPLA A G	0.999	**8**	0	0	0
PANN A G	0.999	**8**	0	0	0
NNOC A E	**0.017**	0	**63**	1	0
NNOC J E	**0.030**	0	**58**	2	0
CLUT A S	0.411	4	**49**	16	2
CLUT A E	0.255	6	**43**	12	2
CLUT J E	0.340	11	17	**41**	0
GAFF J S	0.754	8	34	**38**	12
LMEG J E	0.371	28	2	**38**	3
CLUT J S	0.446	8	26	**37**	3
PVIG J E	0.785	16	0	**33**	21
GAFF A S	0.725	19	8	**30**	31
PVIG A E	0.622	12	1	**30**	4
PVIG J S	0.921	11	25	**28**	24
NVOL J S	0.315	0	0	**27**	0
LMEG A E	0.830	17	5	**19**	0
LUMB A E	0.481	0	0	**14**	0
LUMB J E	0.481	0	0	**14**	0
EGRA A E	0.491	0	0	**14**	0
LUMB J S	0.979	5	**7**	**7**	0
LMAC J E	**0.010**	7	0	5	**83**
LSPP J S	**0.001**	16	0	4	**69**
LMAC A S	**0.044**	0	0	0	**49**
LMAC J S	0.279	5	0	4	**40**
PVIG A S	0.568	14	4	27	**34**

TABLE 15.? Indicator values for fishes based on their relative abundance and frequency of occurrence in unchannelized or channelized reaches of the South Sulphur River. Proportions of Monte Carlo randomized trials (1000) having indicator value equal to or exceeding those observed is given for each species. Bold font designates highest indicator value for each species and species that are significant indicators of a particular reach.

		Reach	
Species	P	Unchannelized	Channelized
CLUT S	**0.003**	**96**	4
PVIG E	**0.010**	**94**	5
CLUT E	0.073	**88**	8
GAFF S	**0.003**	**86**	11
PVIG S	**0.003**	**86**	12
LMEG E	**0.023**	**85**	10
LMAC E	0.448	**78**	22
IBUB G	0.617	**70**	30
NNOC E	0.059	**67**	0
GAFF E	0.326	**67**	27
LSPP S	0.275	**61**	23
LCYA E	0.653	**50**	33
LMAC S	0.614	**42**	11
LSPP E	0.579	**41**	9
EGRA E	0.969	**37**	**37**
ICYP G	0.435	**33**	0
LUMB S	0.435	**33**	0
IPUN G	0.478	**33**	0
NVOL S	0.478	**31**	1
POLI G	0.725	**28**	3
CARP G	0.999	**20**	13
LUMB E	0.999	**17**	0
LHUM E	**0.023**	1	**79**
LOSS G	0.069	3	**66**
CCAR G	0.999	6	**20**
DCEP G	0.999	0	**17**
LPLA G	0.999	0	**17**
PANN G	0.999	0	**17**

TABLE 16.? Indicator values for juvenile and adult fishes based on their relative abundance and frequency of occurrence in unchannelized or channelized reaches of the South Sulphur River. Proportions of Monte Carlo randomized trials (1000) having indicator value equal to or exceeding those observed is given for each species. Bold font designates highest indicator value for each species and species that are significant indicators of a particular reach.

		Reach	
Species	P	Unchannelized	Channelized
CLUT A S	**0.000**	**99**	1
PVIG J E	**0.013**	**94**	5
CLUT J S	**0.000**	**93**	6
PVIG A E	**0.012**	**93**	6
GAFF J S	**0.000**	**92**	6
PVIG A S	**0.000**	**86**	12
PVIG J S	**0.000**	**86**	12
LMEG J E	**0.021**	**86**	10
CLUT J E	0.078	**82**	12
GAFF A S	**0.002**	**80**	17
CLUT A E	**0.040**	**79**	3
LMAC J E	0.415	**78**	22
LMEG A E	**0.049**	**70**	5
LSPP J S	0.245	**61**	23
GAFF J E	0.385	**61**	22
IBUB A G	0.787	**56**	32
GAFF A E	0.409	**55**	30
LCYA J E	0.509	**54**	29
NNOC J E	0.194	**50**	0
NNOC A E	0.198	**50**	0
LMAC J S	0.616	**42**	11
LSPP J E	0.575	**41**	9
IPUN A G	0.449	**33**	0
ICYP A G	0.476	**33**	0
LUMB J S	0.476	**33**	0
CARP A G	0.999	**20**	13
POLI A G	0.735	**28**	3
IBUB J G	0.448	**29**	2
LMAC A S	0.999	**15**	2
NVOL J S	0.449	**31**	1
EGRA A E	0.999	**17**	0
LUMB A E	0.999	**17**	0
LUMB J E	0.999	**17**	0
LHUM J E	**0.009**	0	**83**
LCYA A E	0.506	25	**52**
LOSS J G	0.171	0	**50**
LOSS A G	0.226	5	**47**
EGRA J E	0.882	33	**42**
LHUM A E	0.392	5	**35**
LMAC A E	0.445	0	**33**
CCAR A G	0.999	6	**20**
DCEP A G	0.999	0	**17**
LPLA A G	0.999	0	**17**
PANN A G	0.999	0	**17**

DISCUSSION

Based on Schlosser's model of Jordan Creek (Schlosser 1987), I hypothesized that habitat heterogeneity would be greater in the unchannelized (as compared to channelized) reach of the South Sulphur River, which would therefore have more stable fish assemblages. Fish assemblages in this reach would have similar total fish density and higher species richness, in addition to lower density and higher biomass of larger-bodied fish (primarily piscivores and omnivores), as well as lower density and biomass of juveniles and adults of small-bodied species (primarily invertivores) as compared to the channelized reach. Whereas habitat heterogeneity conformed to predictions, results for others did not, and in fact, results for species richness and trophic biomass were opposite of my hypotheses. These predictions of assemblage structure were based on assumptions regarding processes and mesohabitat characteristics and the corresponding ecological responses of fish species. This system has been anthropogenically modified beyond just channelization. Levees, dams, agricultural runoff, limited riparian vegetation, and tributaries that have been cut off from the main channel were factors in the unchannelized reach as well as the channelized reach. My results indicate that these factors and their influence on stream processes and habitat contributed to discrepancies between observed and predicted results for fish assemblage structure.

Habitat Characteristics

Although the channelization of the South Sulphur River occurred almost 50 years before my study, previously altered stream channels may never regain their prior level of habitat diversity (Gregory et al. 1994). Therefore, as expected following the Schlosser (1987) model, habitat heterogeneity in the unchannelized (upstream) reach of the South Sulphur River was greater as compared to the channelized (downstream) reach. Total habitat heterogeneity (3.14) at site 1 in my unchannelized reach was similar to the reach in Jordan Creek that had highest pool development (3.15). Heterogeneity in sites 2 and 3 (2.95 and 2.91) in my unchannelized reach, and site 4 (2.45) in my channelized reach was similar to that in Jordan Creek (2.84) that had intermediate pool development. Heterogeneity in sites 5 and 6 (2.08 and 1.76) in my channelized reach was similar to the modified upstream reach (2.07), which had the least pool development in Jordan Creek. However, the model strongly relied on pool development, especially with regard to depth. Overall, both reaches had moderate to deep water, very slow currents, and silty substrate.

The variety of mesohabitat types was greater in the unchannelized reach as it contained pools, riffles, runs, and backwaters, whereas the channelized reach comprised almost entirely pool habitat, no riffles or backwaters, and only one site included a run, which formed in summer 2002. Not all mesohabitats persisted at every site across years. In the unchannelized reach, pools and runs were common in all sites during each collection, but presence of riffles and backwaters differed across sites and years. Riffles were consistently present at site 1, but only occurred during summer 2001 at site 3, and never at site 2. Backwaters only occurred at site 3 and were present in both years. Well-developed riffle-pool patterns persisted at Site 1, but were less-well developed at sites 2 and 3, where pools were only slightly better developed (deeper) than those in the channelized reach. Unlike Jordan Creek (Schlosser 1987), the range of depths in all sites of the South Sulphur River included those that were not limiting for large-bodied species of both omnivores and piscivores.

Scores for habitat quality included both instream and riparian metrics. As expected, overall instream habitat quality was lower in the channelized reach and reflected channel alteration, reduced sinuosity, and greater sediment deposition. Pool variability (high scores indicating mix of large, small, shallow and deep pools) scored highest (12) for site 1 in the unchannelized reach, and lowest (4) for site 4 in the channelized reach, but was similar across other sites (ranging from 5 to 7). Thus, pools were only slightly more developed in unchannelized than those of the channelized reach. Scores for riparian vegetation were similar and high to moderate across all sites. However, the overall total score for habitat quality in the unchannelized reach was reduced due to lower scores for bank stability (raw areas with high erosion potential during floods) at sites having high sinuosity. Thus, despite the presence of levees to protect agricultural areas in the unchannelized reach, some evidence was present of the natural tendency for streams in this region to form oxbows.

Fish Assemblage Structure

Because many species of fish exhibit strong association with certain types of habitat, stream reaches with higher habitat heterogeneity can be expected to have greater species richness than reaches with fewer habitats for fishes to exploit (Gorman and Karr 1978; Schlosser 1982a; Angermeier and Karr 1984; Reeves et al. 1993). However, my results showed that despite higher habitat heterogeneity in the unchannelized reach, species richness was similar to that in the channelized reach. Other studies conducted on the South Sulphur River (Carroll et al. 1977, Capone and Kushlan 1991) reported similar results. Carroll et al. (1977) found no difference in species richness between unchannelized and channelized reaches of the South Sulphur River, and Capone and Kushlan (1991) were unable to predict species density (number of species per area) based on habitat heterogeneity, in contrast to predictions of the conceptual model proposed by Schlosser (1987).

Of the total number of species collected in the South Sulphur River, approximately half were classified as tolerant species, and although there were more in the channelized than unchannelized reach, the actual difference was small (9 versus 8). Linam and Kleinsasser (1998) classified tolerant species as those that typically show increased distribution and abundance despite historical degradation of their environment and tend to be the dominant species in disturbed habitats. Tolerant species that were dominant in the channelized reach were gizzard shad, longnose gar, shortnose gar, and river carpsucker, which all occur primarily in sluggish, pool habitats (Robison and Buchannan 1988). Tolerant species that were dominant in the unchannelized reach were western mosquitofish, red shiner, and bigmouth buffalo, which occur across a wide variety of habitats. Species such as red shiner are considered tolerant and habitat generalists that inhabit a variety of habitat conditions. However, in my study (during summer low-flow conditions) they were more abundant and occurred most often in faster moving run and riffle habitats. Intolerant species are those that are sensitive to environmental conditions and are typically the first to disappear following a disturbance. There were two intolerant species in my study—freckled madtom, and mimic shiner. Both species were more associated with the unchannelized than the channelized reach and generally occupy riffle habitat having gravel substrates (Orth and Maughan 1982; Robison and Buchanan 1988), both of which were only found in the unchannelized reach. Freckled madtom, although a significant indicator of riffle habitat, was not a significant indicator of the unchannelized reach because it occurred in too few of those collections.

Schlosser (1987) predicted a peak in density of fish in habitats intermediate between homogeneous, shallow habitats—his channelized reach—and heterogeneous habitats that included deeper pools—his downstream, natural reach. I found higher density of fishes overall in the unchannelized reach of the South Sulphur River, and relative density of certain species differed between reaches. Red shiner, western mosquitofish, bullhead minnow, and longear sunfish were indicators of the unchannelized reach whereas, orangespotted sunfish was the only indicator of the channelized reach. Bluegill and juvenile sunfish were indicators of backwater habitat, which only occurred in one unchannelized site, and therefore, it was not an indicator of the unchannelized reach.

Fish-Habitat Relationships

During summer low-flow conditions in the South Sulphur River, juveniles and adults of most species were collected in the same mesohabitats and reaches. Perhaps this was due to reduced habitat volume and lower opportunity for habitat segregation among life stages, or to the large proportion of habitat generalists in the fish assemblage. With regard to distribution of body size and trophic-group biomass in channelized versus natural reaches, my results were directly opposite of those predicted by the Schlosser (1987) model. In the unchannelized reach, there were more small-bodied fishes (primarily invertivores) and fewer large-bodied omnivores (channel catfish) and large-bodied predators (white crappie and flathead catfish), but the predators were not small juveniles of large-bodied species, as was found in Jordan Creek. In neither reach of the South Sulphur River was depth limiting to the distribution of large-bodied fishes (omnivores and piscivores), as compared to Jordan Creek, where channelized reaches were too shallow to support large fishes. Compared to the unchannelized reach, the channelized reach of the South Sulphur River had fewer small-bodied fishes, more and larger omnivores (river carpsucker and gizzard shad), and more piscivores (primarily gar). With regard to life-history characteristics of assemblages in each reach of the South Sulphur River, my results also opposed the trend predicted by Schlosser. In the Schlosser model, assemblages corresponding to homogeneous, channelized habitats contained more fishes with colonizing life-history attributes—prolonged breeding seasons, higher population growth rates, and greater dispersal capability of young—as compared to the more heterogeneous, unchannelized habitat, which had more fishes adapted to less-variable (more stable) conditions—longer time to maturity, shorter reproductive season, and lower population growth rates.

Discrepancies in results as compared to Schlosser (1987) are probably related to several factors. This system had been heavily modified by activities other than just channelization. For both reaches, these included an upstream dam, levees, reduced vegetation in riparian zones, agricultural runoff, and frequent (approximately two per year from 1997 to 2001) fish kills (Adam Whisenant, biologist for Texas Parks and Wildlife, unpublished data), each of which can affect the structure of fish assemblages (Sharpe et al. 1984; Bryan and Rutherford 1993; Gafny et al. 2000). This system was originally channelized in the 1950's and fish assemblages might have experienced some recovery in the last half century. There were also regional differences in stream systems and faunal composition as compared to Jordan Creek. Many of the species collected in the South Sulphur River have prolonged breeding seasons, and my summer samples would have included breeding individuals and young fishes, which would have contributed to reversed trends in fish density and biomass compared to Jordan Creek. If habitat volume was temporarily reduced during summer low-flow, then fish might have been forced into suboptimal habitat, thus increasing habitat overlap between juveniles and adults, as well as piscivores and their smaller-bodied prey. In addition, many conclusions regarding the model (Schlosser 1987) were based on results for temporal variation in seasonal patterns, which was not addressed in my study.

Schlosser's model relied on spatial variation in depth and habitat volume, which set the habitat template for the important biotic processes of predation and competition that were primary forces controlling fish assemblage structure. This was especially the case for the natural reach of Jordan Creek, where temporal environmental variability and stochasticity were less important as compared to factors in the shallow channelized reach, which was more temporally variable. Harsh summer conditions can limit the ability of larger and less tolerant fish to persist in streams (Matthews and Styron 1981). Results of my summer low-flow sampling in the South Sulphur River more strongly support abiotic factors and processes as the primary forces structuring fish assemblages. In particular, the large number of tolerant species and habitat generalists in the South Sulphur River suggests that physicochemical factors are important and that the system experiences considerable environmental variation.

Fluctuations in flow can eliminate juveniles and smaller species from pools (Harvey 1987), and over the short term these habitats may never approach a stable state. Stream flows in this region are highly variable relative to the long-term mean. There is a predictable wet season (November-April) and a dry season (May-October), but floods and droughts are unpredictable within those seasons. Capone and Kushlan (1991) also found that physical processes such as stream morphology and highly unstable, temporally variable stream flows were more important regulators of Sulphur River fish assemblages among pools than were biotic factors such as predation and competition, and suggested that northeast Texas streams possibly represent the extreme left of Schlosser's (1987) hypothesized model.

In addition to the unpredictable nature of the natural flow regime for streams in the area, Cooper dam was recently constructed in 1991 a short distance upstream from the unchannelized sites sampled in this study. While fish assemblages may have experienced some recovery from past channelization, Cooper dam is a relatively recent addition to the system, and fish assemblages might still be adjusting to this change in their environment thus contributing to differences from the Jordan Creek model. Flow management in regulated reaches has major impacts on local hydraulic conditions, which influence species abundance and fish diversity (Gorman and Karr 1978; Orth and Maughan 1982). Water release and retention can have a larger influence on the variability of local streamflows and fish assemblages in reaches relatively close to a dam (as in the unchannelized reach) as opposed to those located a significant distance downstream (as in the channelized reach) (Kinsolving and Bain 1993).

Species that inhabit streams with large environmental variability have evolved to cope with disturbance in areas where environmental conditions can be extreme and somewhat unpredictable (Poff and Ward 1990). Many of these species can readily inhabit a variety of habitats and still thrive, and thus they are considered habitat generalists. The Sulphur River Basin is composed largely of habitat generalists, many of which are classified as tolerant. The abundance of tolerant habitat generalists in this system suggests a fish assemblage that has adapted to persist through harsh environmental conditions. This pattern is seen in other variable warmwater streams throughout the country (Matthews 1987; Meador and Matthews 1992; Kinsolving and Bain 1993; Poff and Allen 1995; Matthews 1998). South Sulphur River fish assemblages have evolved to inhabit areas with extreme environmental changes due to physical influences, including not only droughts and floods, but also fluctuations in chemical influences such as dissolved oxygen, pH, temperature, agricultural runoff and anoxic dam releases. However, flow regime is likely the most influential environmental factor in streams of this region.

Fluvial specialists can be described as those species that require flowing water for much of their life cycle. Very few fluvial specialists are currently present in the Sulphur River Basin. Intolerant fluvial specialists (such as freckled madtom and mimic shiner) have narrow ranges of habitat use. My results suggest that these species occur more frequently in unchannelized areas. Several previously common species of fish have been reduced in number or have been extirpated (Garrett 1999), and other rare or non-native forms have increased in abundance. Species such as the paddlefish (*Polyodon spathula*), taillight shiner (*Notropis maculatus*), and orangebelly darter (*Etheostoma radiosum*) were previously documented in these areas before anthropogenic modifications to the stream caused their numbers to decline dramatically such that they now are under various levels of protection (Garrett 1999). These species are dependent on riffle habitats for various life history stages, probably removed during channel modifications.

Access to all areas of the stream is restricted mainly to bridge crossings. Access by boat to many areas of the stream was difficult due to low flows and some were impassable due to large accumulations of woody debris. Because of these factors, study sites were chosen based upon access rather than random placement. Therefore, it gives a somewhat biased view of the river. Lack of persistent mesohabitats may also have hampered the ability of my study to reflect accurately South Sulphur River fish assemblages. Further study concentrating on the variability of flow should be done particularly on the effects of drought and floods. Effective management should include identification of fluvial specialists and habitat suitability requirements for those species. Whenever possible, release of water from Cooper dam should reflect the instream flow needs of these species.

CONCLUSIONS

My results did not conform to the conceptual model proposed by Schlosser (1987). His study focused on biotic processes more than the abiotic effects of a highly stochastic environment. I propose that abiotic processes, particularly extreme fluctuations in flow regimes, are likely to be the most influential factors affecting fish assemblages in the South Sulphur River. Streams in this region are naturally subject to extreme variations in streamflow, but unchannelized sites may have been more directly influenced by water release or retention from the relatively recent construction of Cooper Dam located just upstream, whereas channelized sites, located much further downstream, were probably less affected. Most fish species present in the South Sulphur River are considered habitat generalists, have evolved to cope with extreme changes in environmental conditions, and are able to populate a variety of available habitats. Therefore, future management of this stream should reflect the needs of the few remaining fluvial specialists in this system, such as the intolerant freckled madtom and mimic shiner.

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