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Biodiversity Patterns of Littoral Tidal River Fishes in the Gulf Coastal Plain Region of Mississippi

CHET F. RAKOCINSKI, MARK S. PETERSON, STEVEN J. VANDERKOOY, AND GREGORY J. CREGO

Fish biodiversity patterns within littoral habitats of major tidal river systems of coastal Mississippi were examined. The biodiversity of littoral tidal river fishes varied meaningfully on several spatial scales in the Gulf Coastal Plain region of Mississippi. Fish diversity typically appeared higher in littoral channel habitats than in side-pond habitats of tidal river systems. Faunal representation by three core groups of littoral fishes (cyprinids, centrarchids, and fundulids) generally differed between side-pond and channel habitats, as well as among different tidal river systems. Some of the faunal variation among systems reflected biogeographic (east/west) trends, but most of the variation reflected system size-related patterns. Among-site similarity in fish assemblage composition reflected both site proximity and system size. Moreover, the degree of variability in assemblage composition increased with system size. Thus, regional assemblage patterns were generally most discernible on the landscape scale, rather than through historical congruence. This limited regional study of tidal river fish biodiversity improved our biogeographic understanding by revealing the importance of landscape-scale factors such as tidal river size and associated variation in the available species pool. Understanding landscape-scale environmental variation is key to explaining regional fish diversity patterns.

Biodiversity patterns for tidal river fishes of the Gulf Coastal Plain region are poorly known (Livingston, 1992). Knowing whether current biodiversity patterns reflect mostly historical factors related to dispersal or recent ecological factors is key to understanding the biogeography of riverine fishes (Mayden, 1992). Biodiversity patterns are expressed through nested scale-dependent variation (Powell, 1995), as influenced by both historical and ecological factors. Hierarchical approaches are increasingly being used to understand scaling effects and linkages among different levels of ecological organization (Levin, 1992; Wu and Loucks, 1995). A hierarchical perspective on riverine fish biodiversity can distinguish scale-dependent patterns in community structure as expressed spatially at regional, landscape, or habitat levels (Jackson and Harvey, 1989; Tonn, 1990; Tonn et al., 1990; Schlosser, 1991; Grossman et al., 1995; Poff and Allan, 1995; Lyons, 1996).

Current biodiversity patterns of Gulf Coastal Plain rivers were in part produced by historical fluctuations in sea level with attendant opportunities for dispersal, extinction, speciation, and adaptation (Conner and Suttkus, 1986; Swift et al., 1986; Boschung, 1992). Caldwell (1966) pointed out that river systems along the Gulf coast were zoogeographically important with regard to the dispersal of fishes and, fur-

thermore, that the Biloxi Bay and Bay of Saint Louis river systems fall "in the zone of faunal change between the Mississippi River and the Mobile Basin." He postulated that the Biloxi Bay and Bay of Saint Louis systems of the Mississippi Gulf coast were "tributary" to a larger common riverine system during the low sea levels of the Pleistocene and that most of the fishes now inhabiting both systems would have had unrestricted access to a common "trunk river" in the past. During this time, Mississippi Coastal Plain river systems typically emptied 20–30 km east of their present mouths (Swift et al. 1986). Swift et al. (1986) also pointed out that the smaller Mississippi Gulf coastal systems lacked certain characteristic large-river taxa and noted that adjacent lowland streams, such as those within our study region, typically contain similar faunas. However, they did notice an overall east-to-west decrease in the number of fish species below the fall line, which they attributed to lower numbers of fishes in "stream-adapted" families, including catostomids, cyprinids, and percids. Based on mtDNA and distributional information, Birmingham and Avise (1986) noted that fish faunas from Gulf of Mexico systems were more differentiated from each other than were faunas from rivers entering the Atlantic.

The general objective of this study was to examine fish biodiversity patterns within littoral

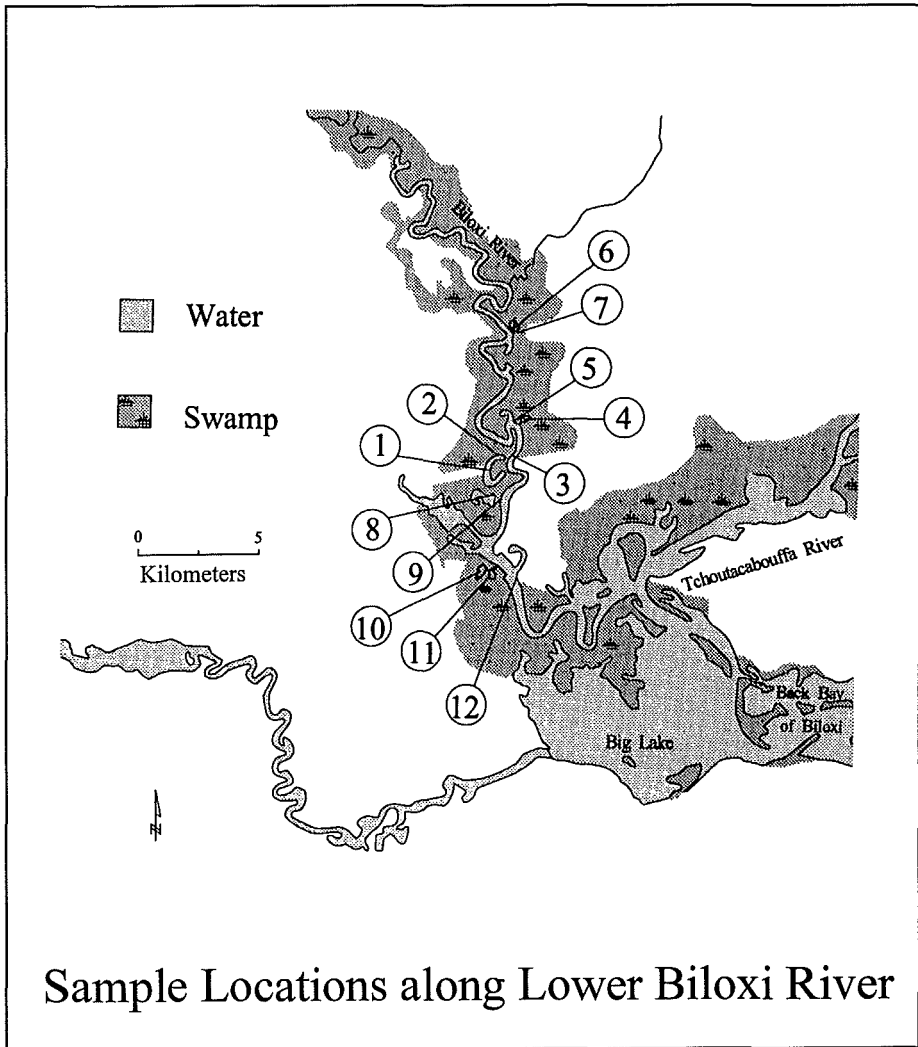


Fig. 1. Map of lower portion of Biloxi River showing system landscape features, including locations of pond and channel sites.

habitats of major tidal river systems of coastal Mississippi. We will focus on three specific objectives contributing to a regional perspective of littoral fish biodiversity in coastal rivers (1) by comparing fish biodiversity between littoral side-pond and littoral channel habitats of tidal rivers across the Mississippi Coastal Plain region, (2) by comparing fish faunas among various coastal river systems, and (3) by characterizing tidal river fish assemblages within a regional framework.

STUDY AREA

Surrounding floodplain marshes combine with channels and side-ponds to form the wa-

tershed landscape in the northern Gulf coast region. Numerous side-ponds scattered along winding lower portions of coastal river systems represent a major landscape feature (Fig. 1). Side-ponds vary in the degree to which they are cut off from the main channel, as well as in their sizes, their shapes, and the composition of their fringing vegetation. Most side-ponds are remnant mainstem channel segments, usually connected by one or two small openings (<2 m wide) to the main channel. Such natural connections between side-ponds and main channels may act as conduits between side-pond and channel habitats. However, pond and channel littoral habitats can be readily distinguished by such variables as cur-

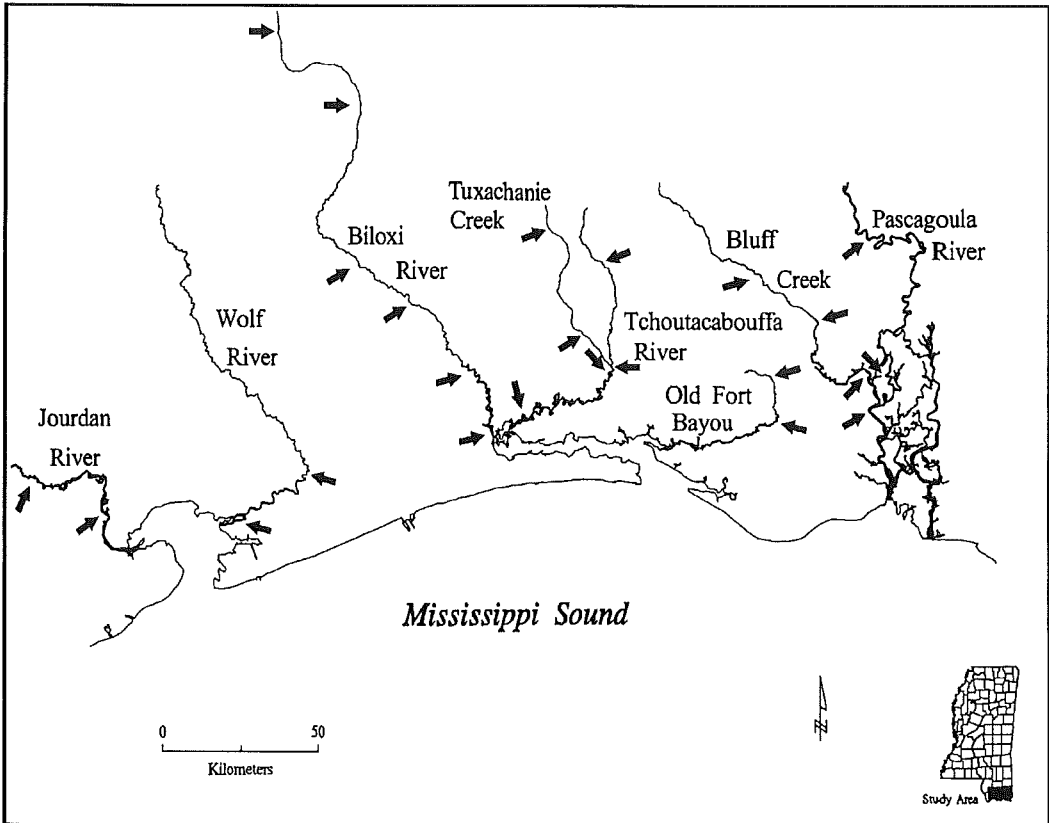


Fig. 2. Map of study area showing reaches sampled within various river systems, as delineated by arrows. Multiple sites were sampled within each reach as described in the text.

rent velocity, submerged aquatic vegetation (SAV) composition and amount, pH, substratum, turbidity, etc. (Peterson et al., 1996; Peterson and VanderKooy, 1997).

During the summers of 1993–95, we conducted a regional survey including 131 standard fish collections from 74 channel and 57 side-pond sites within eight Mississippi coastal river systems (Fig. 2). Sites were distributed across the Mississippi coast from east to west: in the Pascagoula River (9 pond, 5 channel), Bluff Creek (10 pond, 7 channel), Old Fort Bayou (10 pond, 6 channel), the Tchoutacabouffa River (8 pond, 13 channel), Tuxachanie Creek (16 channel), the Biloxi River (7 pond, 17 channel), the Wolf River (7 pond, 4 channel), and the Jourdan River (6 pond, 6 channel) (Table 1). Sites were located mostly near the coast within the lower portions of river systems, although some stream sites also were sampled (e.g., Tuxachanie Creek). Sampled watersheds encompassed a wide range of drainage area sizes, broadly categorized as small (<259 km²), medium (259–1,295 km²),

or large (>2,590 km²) river systems (Mike Runner, USGS, Jackson, MS, pers. comm.). By this classification, Bluff Creek, Old Fort Bayou, and Tuxachanie Creek represented small systems; the Biloxi, Jourdan, Tchoutacabouffa, and Wolf rivers represented medium systems; and the Pascagoula River represented a large system. In this paper, we follow the hierarchical watershed classification of Jenkins et al. (1971), by which all of our tidal river sites fall within the system category (i.e., a group of interconnected streams within a drainage).

METHODS

Each site was visited once during the 3 yr of sampling. We sampled fishes from unaltered side-pond and channel littoral habitats in Bluff Creek and Old Fort Bayou 12–16 July 1993; from Tchoutacabouffa and Biloxi Rivers 13–16 and 25 July 1994; from the Wolf and Jourdan rivers 26–30 July 1994; from lower Bluff Creek and mainstem Pascagoula River 8–14 Aug. 1995, and from additional upstream sites from

TABLE 1. Site collections during summers of 1993, 1994, and 1995, by system from west to east. Sites are numbered consecutively from upstream to downstream, including both channel and side-pond sites. Channel collections excluded from the final CA ordination comprised those marked by an asterisk (see *Methods*) (# = collections lacking any fishes; collections marked with A or B represent unique sites within the same pond; 93 = 1993; 94 = 1994; 95 = 1995).

Jourdan River	Wolf River	Biloxi River	Tuxachanie River	Tchoutacabouffa River	Old Fort Bayou	Bluff Creek	Pascagoula River
Channel sites							
Site 02, 94	Site 03, 94	Site 02, 94	Site 01, 95*	Site 02, 94	Site 02, 93	Site 02, 93	Site 02, 95
Site 04, 94	Site 06, 94	Site 03, 94	Site 02, 95*	Site 03, 94	Site 04, 93	Site 03, 93	Site 05, 95
Site 06, 94	Site 07, 94	Site 05, 94	Site 03, 95*	Site 06, 94	Site 06, 93	Site 08, 93	Site 07, 95
Site 08, 94	Site 11, 94	Site 09, 94	Site 04, 95*	Site 07, 94	Site 07, 93	Site 10, 93	Site 10, 95
Site 10, 94		Site 12, 94*	Site 05, 95*	Site 09, 94	Site 10, 93	Site 11, 93	Site 11, 95
Site 11, 94		Site 13, 95*	Site 06, 95#	Site 12, 94*	Site 11, 93	Site 14, 95*	
		Site 14, 95*	Site 07, 95*	Site 13, 94*		Site 16, 95*	
		Site 15, 95	Site 08, 95*	Site 16, 95*			
		Site 16, 95	Site 09, 95	Site 17, 95*			
		Site 17, 95	Site 10, 95	Site 18, 95*			
		Site 18, 95	Site 11, 95#	Site 19, 95*			
		Site 19, 95	Site 12, 95*	Site 20, 95*			
		Site 20, 95	Site 13, 95	Site 21, 95*			
		Site 21, 95	Site 14, 95				
		Site 22, 95	Site 15, 95#				
		Site 23, 95	Site 16, 95*				
		Site 24, 95					
Side-pond sites							
Site 01, 94	Site 01, 94	Site 01, 94		Site 01, 94	Site 01, 93	Site 01, 93	Site 01, 95
Site 03, 94	Site 02, 94	Site 04, 94		Site 04, 94	Site 03A, 93	Site 04, 93	Site 03, 95
Site 05, 94	Site 04, 94	Site 06, 94		Site 05, 94	Site 03B, 93	Site 05, 93	Site 04, 95
Site 07, 94	Site 05, 94	Site 07, 94		Site 08, 94	Site 05, 93	Site 06, 93	Site 06, 95
Site 09, 94	Site 08, 94	Site 08, 94		Site 10, 94	Site 08A, 93	Site 07, 93	Site 08, 95
Site 13, 94	Site 09, 94	Site 10, 94		Site 11, 94	Site 08B, 93	Site 09, 93	Site 09, 95
	Site 10, 94	Site 11, 94		Site 14, 94	Site 09A, 93	Site 12, 93	Site 12, 95
				Site 15, 94	Site 09B, 93	Site 13, 93	Site 13, 95
					Site 12A, 93	Site 15, 95	Site 14, 95
					Site 12B, 93	Site 17, 95	

the Biloxi River, the Tchoutacabouffa River, and Tuxachanie Creek 6–28 June 1995 (Fig. 2; Table 1). Wherever a side-pond was sampled, an adjacent main channel site also was sampled. Sometimes, larger side-ponds were represented by more than one site within a pond. Sampling biases due to large interannual variation in water levels were unlikely, as rainfall amounts were nearly normal during all 3 yr of this study. Monthly rainfall amounts between March and August never deviated by more than 11.5% from corresponding monthly values averaged over the previous 30 yr (NOAA, National Climatic Data Center, Asheville, NC, 1993–95). Furthermore, on only one of the 26 sampling dates during the 3-yr study did rainfall amounts exceed 1.4 cm.

Littoral habitats were systematically characterized at all sites by first collecting physicochemical data. Water quality measurements were all made 10 cm below the water surface and included water temperature (± 0.5 C), dissolved oxygen (DO) (± 0.1 mg/l), turbidity ($\pm 2\%$ NTU), pH (± 0.02), conductivity ($\pm 2\%$ μ mho), and current velocity (± 0.03 m/sec). Other recorded habitat features included substratum, litter amount, cover amount (e.g., branches, trees, etc.), SAV (% cover), and emergent aquatic vegetation (EAV) (% cover). Litter amount and other structure categories were scored as 1 (absent), 2 (intermediate), or 3 (high amounts) (Ross et al., 1987). Substratum was scored as 1 (mud/silt), 2 (very fine–fine sand), 3 (medium sand), or 4 (coarse–very coarse sand), as an ordinal modification of the Wentworth size-class scale (Folk, 1980). Macrophyte coverage (%) was visually estimated.

Littoral fishes were thoroughly and consistently sampled from shallow (i.e., <1.5-m-deep) shoreline habitats at each site, by consecutively using three collecting techniques throughout the same area of 8.0–9.0 m²: (1) a Smith-Root backpack electroshocker; (2) a 46 \times 53-cm heavy dip net lined with 3.1-mm-mesh netting; and (3) a 3.0 \times 1.2-m bag seine constructed of 3.1-mm-mesh netting. Electroshocking time was held to ca. 3 min (mean range, 2.44–3.10 min). After electroshocking, two persons dipnetted and then pulled the bag seine through the entire area. These three techniques used in this exact sequence provided comparable censuses of littoral fishes from each site. All sampled fishes were fixed in 10% formalin for 1 wk and were then transferred to 50% isopropanol. In the laboratory, fishes were identified to species, enumerated by collection, and curated either in the Mississippi State University (MSU) Ichthyological Collec-

tion or in the Gulf Coast Research Laboratory (GCRL) Museum.

Data analysis.—Rarefaction point estimates reflecting the relationship between species richness and the total number of fishes collected were plotted to compare fish biodiversity between channel and pond collections from each river system. For three dominant core groups of littoral fishes including cyprinids, centrarchids, and fundulids, the proportionate representation of total abundance and total species richness was also plotted for both channel and pond collections within each system and examined for large-scale spatial patterns.

Multivariate analyses were performed using the Community Analysis System (CAS 5.0) (Bloom, 1994). A preliminary cluster analysis of sites using ρ th root of abundance, a similarity matrix based on the proportional similarity index, and the group average sorting algorithm indicated that littoral fish faunas of pond and channel collections were usually dissimilar. Thus, correspondence analysis (CA) ordinations were performed separately for pond and channel collections.

Results of the CA (Pielou, 1984) were used to plot species' centers of abundance and site coordinates in a mutually referential ordination space. The dispersion of site coordinates coded by system to convey biogeographic information was plotted within the first three dimensions of CA space. The proximity of site coordinates reflected the degree of faunal similarity, while the proximity of species coordinates reflected their tendency to co-occur in collections. The CAS performed CA by doing a simultaneous double standardization and subsequent multiplication of the original data matrix by its transpose. Determination of the species coordinates was accomplished with an inverse CA of the original data, yielding ordinations of both sites and species within the same eigen system (Bloom, 1994). We routinely included all species falling within 99% of the total abundance in CA ordinations. Thus, 32 major taxa of the original 48 were retained in the final CA ordination of the 57 pond sites.

Owing to the effect of position in the watershed, the inclusion of all channel collections within the CA ordination produced a site ordination exhibiting a strong arch effect (Gauch, 1982). To focus the CA analysis of channel sites along coastal longitudinal position rather than on watershed position, we excluded sites falling on one side of the tight arch resulting from the inclusion of all the channel collections from a preliminary CA

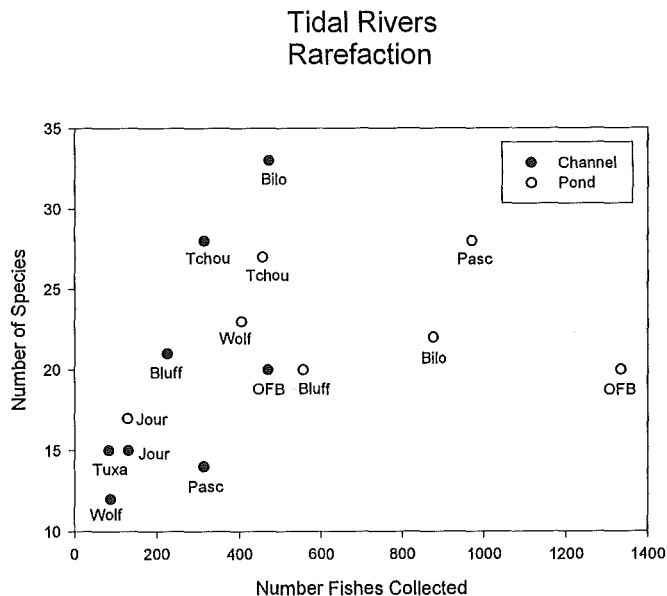


Fig. 3. Rarefaction point estimates of the accumulated number of species vs the total number of fishes, by river system for pond and channel sites. River system codes: Jour = Jourdan River; Wolf = Wolf River; Bilo = Biloxi River; Tuxa = Tuxachanie Creek; Tchou = Tchoutacabouffa; OFB = Old Fort Bayou; Bluff = Bluff Creek; Pasc = Pascagoula River.

(Table 1). Consequently, we excluded seven upper Tuxachanie Creek sites, two upper Biloxi River sites, and eight upper Tchoutacabouffa River sites. Four more outlier sites were excluded during two subsequent ordinations representing two lower Bluff Creek sites and two more Tuxachanie Creek collections. The final channel CA ordination thus included 49 sites. Again, in the inverse CA, we included all species falling within 99% of the total abundance made up by the ordinated sites. *Dormitator maculatus* was also omitted from the final channel site ordination, because it constrained the dispersion of other species coordinates. The final CA ordination of channel sites thus included 49 site coordinates and species coordinates representing 31 of 45 fishes. Resulting configurations of both site and species coordinates in the final channel ordination were dispersed widely throughout CA space.

RESULTS

A total of 6,811 fishes was collected, representing 70 fish taxa belonging to 23 families. Rarefaction point estimates of the accumulated species richness vs the total number of fishes collected showed that littoral fish diversity was typically higher in channel than in side-pond habitats (Fig. 3). As a whole, channel

data points fell on a steeper slope than did side-pond data points. Comparisons of points from both types of habitat within the same river system typically showed that channels were more diverse. Littoral side-pond habitats often had relatively well developed habitat structures, whereas littoral channel habitats were more heterogeneous among sites.

Three core groups dominated the total abundance of littoral fishes (68%), including 12 cyprinids (17.2%), 11 centrarchids (31.7%), and eight fundulids (19.4%) (Figs. 4–6). Cyprinids were collectively threefold more abundant in littoral channel habitats than in side-pond habitats, averaging 30.8% vs 9.0% across all systems (Fig. 4). The relative proportion of the fish fauna made up by cyprinids was generally more than twice as high in littoral channel habitats as well, averaging 18.7% of the species richness in channel habitats vs 8.0% in side-pond habitats across all river systems. Although there was no apparent biogeographic east–west trend in the composition of minnows, there did seem to be a pattern based on the relative size of the drainage area, wherein larger systems like the Pascagoula River showed better representation by minnows.

The centrarchid core group included 11 species and comprised 31.7% of the total abundance of fishes. Relative abundances of cen-

Cyprinidae

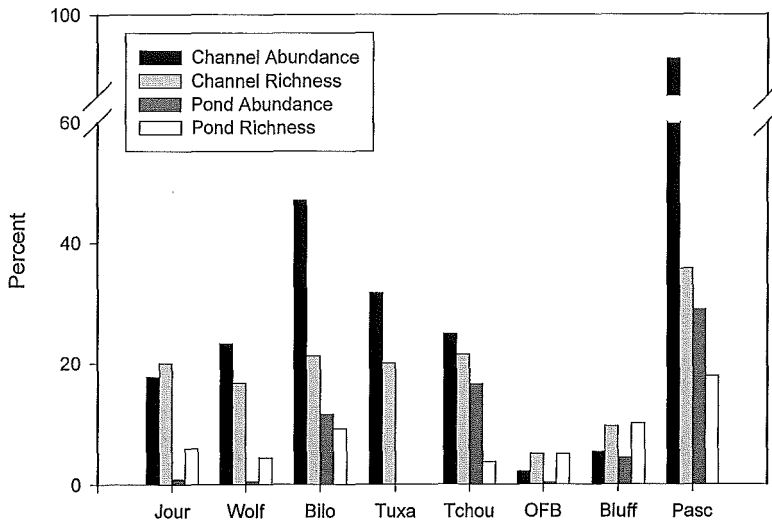
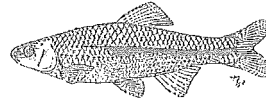


Fig. 4. Proportion of fish fauna represented by cyprinids for pond and channel sites across various river systems arranged from west to east. The cyprinid core group included 12 taxa and comprised 17.2% of the total number of fishes. River system codes follow Figure 3.

Centrarchidae

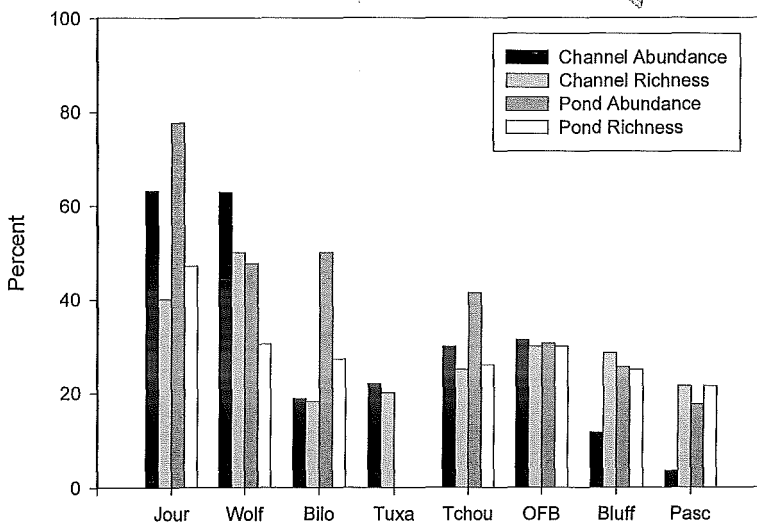
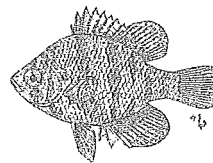


Fig. 5. Proportion of fish fauna represented by centrarchids for pond and channel sites across various river systems arranged from west to east. The centrarchid core group included 11 taxa and comprised 31.7% of the total number of fishes. River system codes follow Figure 3.

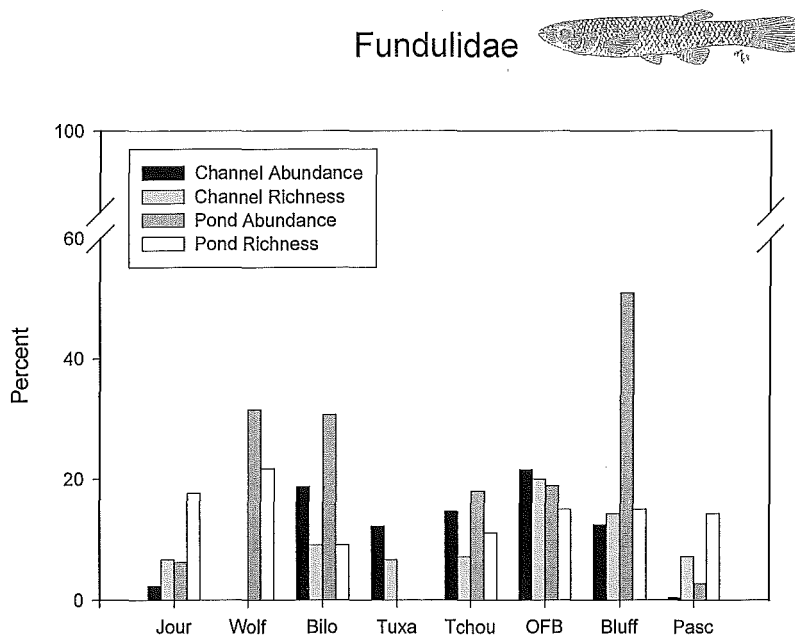


Fig. 6. Proportion of fish fauna represented by fundulids for pond and channel sites across various river systems arranged from west to east. The fundulid core group included eight taxa and comprised 19.4% of the total number of fishes. River system codes follow Figure 3.

trachids were somewhat higher in side-pond habitats than in channel habitats, averaging 41.5% vs 30.4% of the total abundance across all systems (Fig. 5). The relative proportions of the fauna made up by centrarchid species were generally comparable between littoral side-pond and channel habitats, however, averaging 29.6% vs 29.2% of the total species richness across all systems. An east-west biogeographic trend appeared in the faunal makeup of centrarchids, as shown by a declining proportion of sunfish species in a west-to-east direction. This geographic pattern was especially apparent for the side-pond habitats.

The fundulid core group included eight species and comprised 19.4% of the total abundance of fishes. Relative abundances of fundulids were twofold higher in littoral side-pond habitats than in channel habitats, averaging 22.7% vs 10.3% of the total abundance across all systems (Fig. 6). The relative proportions of the fish fauna made up by fundulid species were also higher in side-pond habitats than in channel habitats, averaging 14.8% vs 8.9% of the total species richness across all systems. A fundulid distribution pattern opposite to the cyprinid pattern was evident, with better representation by fundulids in small and medium-sized systems than in large systems.

Eigenvalues from the CA of the pond sites

were 0.77, 0.72, 0.62, and 0.49 for CA axes 1–4, respectively. Cumulative efficiency for the first three axes of the pond CA totaled 36.9% and ranged between 10.8% and 13.5%. The efficiency of the fourth pond CA axis fell off to 8.8%, and 90% of the total variation was accounted for by the first 15 CA axes. Eigenvalues from the final CA for the 49 selected channel sites were 0.87, 0.55, 0.47, and 0.41 for CA axes 1–4, respectively. Cumulative efficiency for the first three axes of the final channel CA totaled 35.0% and ranged between 8.8% and 16.0%. Ninety percent of the total variation for the final channel CA was accounted for by the first 16 CA axes.

The dispersion of side-pond coordinates coded by river system formed three distinct groups within the first three CA dimensions (Fig. 7). A close inspection of this pattern revealed that intercoordinate distances largely reflected the relative degree of site proximity. Thus, sites from the same system often clustered together. Three distinct groups of site coordinates apparently reflected system-size-related variation in associated fish assemblages. Side-pond coordinates from small systems were tightly aggregated, while coordinates from larger systems were more loosely clustered. Coordinates that transgressed this pattern usually represented sites that were in close proximity

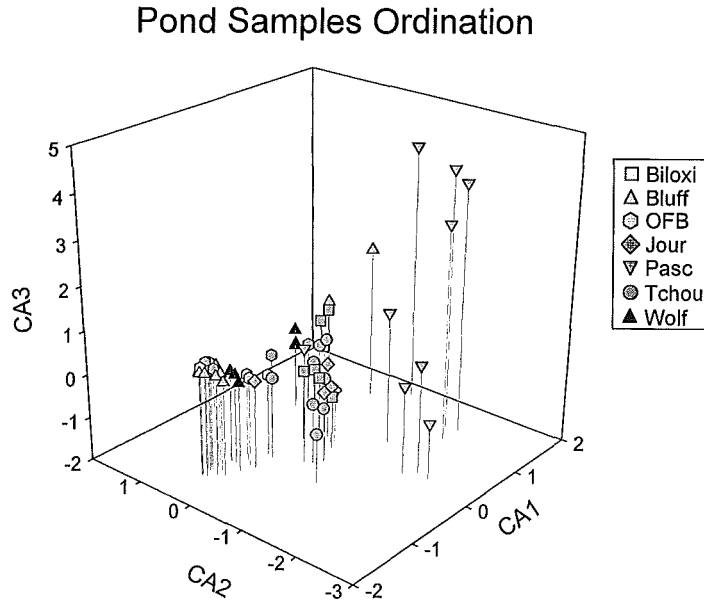


Fig. 7. Side-pond site coordinates within the first three dimensions of CA space, coded by river system to convey biogeographic information. River system codes follow Figure 3.

between two adjacent system segments. Moreover, the degree of scatter in CA site coordinates within clusters increased in conjunction with the system size effect. The trend in the degree of scatter with increasing system size implied parallel increases in among-site habitat heterogeneity and faunal variability.

The dispersion pattern of species coordinates complementary to the pond site coordinates within the first three CA dimensions reflected the co-occurrence of 32 dominant pond fishes (Fig. 8). A tight cluster of CA species coordinates representing a diverse assemblage of typical vegetated side-pond fishes included *Fundulus pulvereus*, *Esox niger*, *Aphredoderus sayanus*, *Etheostoma fusiforme*, *Enneacanthus gloriosus*, *Erimyzon tenuis*, *Fundulus notti*, and *Gambusia affinis*. Several estuarine fishes appearing primarily in side-ponds characteristic of lower portions of medium-sized tidal systems included *Menidia beryllina*, *Syngnathus scovelli*, *Lucania parva*, and *Anchoa mitchilli*. Freshwater taxa characteristic of large tidal river side-pond habitats, such as *Cyprinella venusta*, *Notropis maculatus*, and *Notropis texanus*, were widely spaced in CA ordination space, showing that the fauna of sites within large systems was more variable.

The dispersion of channel coordinates coded by system within the first three CA dimensions also showed a tendency for sites to group by both site proximity and system size (Fig. 9).

However, channel sites aggregated much more loosely than side-pond sites, possibly reflecting relatively greater within-system habitat heterogeneity among the channel sites. For example, Pascagoula River sites were spread out across the entire range of CA axis 2. Sites from small systems clustered within the lower regions of all three CA axes, while the sites from medium systems tended to cluster at higher values of the third CA axis.

The complementary dispersion pattern of channel species coordinates reflected the co-occurrence of the 31 dominant channel fishes (Fig. 10). Species characteristic of vegetated side-pond-like channel habitats of small systems occurred in the region of CA space corresponding with small-system site coordinates, and included *Aphredoderus sayanus*, *Etheostoma fusiforme*, *Enneacanthus gloriosus*, *Erimyzon tenuis*, *Fundulus notti*, and *Gambusia affinis*. Other fish species, characteristic of more estuarine-like habitats of medium-sized rivers, included *Lucania parva*, *Lepomis miniatus*, *Lepomis microlophus*, *Fundulus chrysotus*, *Trinectes maculatus*, and *Notropis petersoni*. Species characteristic of stream habitats formed at least three distinct associations, and included *Notropis texanus*, *Hybognathus nuchalis*, *Cyprinella venusta*, *Notropis longirostris*, *Lythrurus roseipinnis*, *Percina nigrofasciata*, *Ammocrypta beani*, and *Fundulus olivaceus*.

Pond Species Ordination

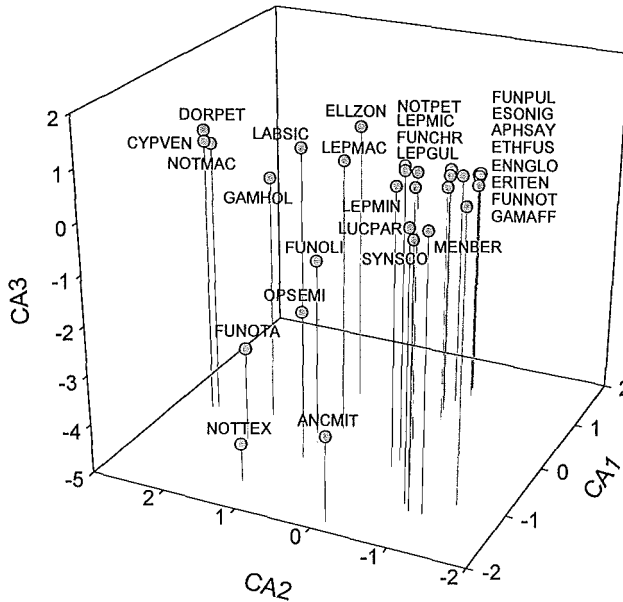


Fig. 8. Species coordinates complementary to side-pond site coordinates within the first three dimensions of CA space for those taxa comprising 99% of the total number of fishes collected from side-pond sites. Species codes: ANCMIT, *Anchoa mitchilli*; APHSAY, *Aphredoderus sayanus*; CYPVEN, *Cyprinella venusta*; DORPET, *Dorosoma petenense*; ELLZON, *Elassoma zonatum*; ENNGLO, *Enneacanthus gloriosus*; ERITEN, *Erimyzon tenuis*; ESONIG, *Esox niger*; ETHFUS, *Etheostoma fusiforme*; FUNCHR, *Fundulus chrysotus*; FUNNOT, *Fundulus notti*; FUNOLI, *Fundulus olivaceus*; FUNOTA, *Fundulus notatus*; FUNPUL, *Fundulus pulvereus*; GAMAFF, *Gambusia affinis*; GAMHOL, *Gambusia holbrooki*; LABSIC, *Labidesthes sicculus*; LEPGUL, *Lepomis gulosus*; LEPMAC, *Lepomis macrochirus*; LEPMIC, *Lepomis microlophus*; LEPMIN, *Lepomis miniatus*; LUCPAR, *Lucania parva*; MEMBER, *Menidia beryllina*; NOTMAC, *Notropis maculatus*; NOTPET, *Notropis petersoni*; NOTTEX, *Notropis texanus*; OPSEMI, *Opsopoeodus emiliae*; SYNSCO, *Syngnathus scovelli*.

Channel Samples Ordination

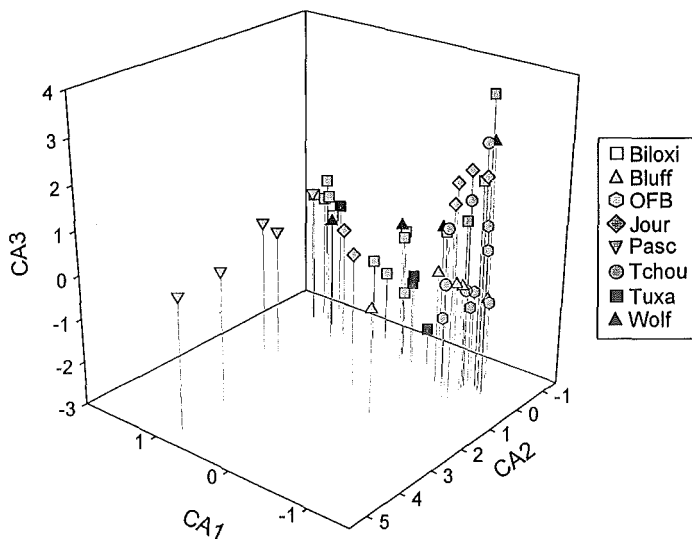


Fig. 9. Channel site coordinates within the first three dimensions of CA space, coded by river system to convey biogeographic information. River system codes follow Figure 3.

Channel Species Ordination

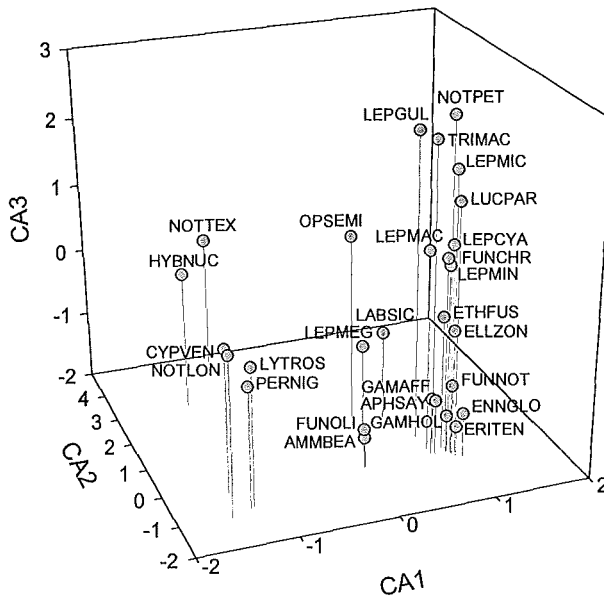


Fig. 10. Species coordinates corresponding to channel site coordinates within the first three dimensions of CA space for those taxa comprising 99% of the total number of fishes collected from channel sites. Species codes: AMMBEA, *Ammocrypta beani*; APHSAY, *Aphredoderus sayanus*; CYPVEN, *Cyprinella venusta*; ELLZON, *Elassoma zonatum*; ENNGLO, *Enneacanthus gloriosus*; ERITEN, *Erimyzon tenuis*; ETHFUS, *Etheostoma fusiforme*; FUNCHR, *Fundulus chrysotus*; FUNNOT, *Fundulus notti*; FUNOLI, *Fundulus olivaceus*; GAMAFF, *Gambusia affinis*; GAMHOL, *Gambusia holbrooki*; HYBNUC, *Hybognathus nuchalis*; LABSIC, *Labidesthes sicculus*; LEPCYA, *Lepomis cyanellus*; LEPGUL, *Lepomis gulosus*; LEPMAC, *Lepomis macrochirus*; LEPMEG, *Lepomis megalotis*; LEPMIC, *Lepomis microlophus*; LEPMIN, *Lepomis miniatus*; LUCPAR, *Lucania parva*; LYTROS, *Lythrurus roseipinnis*; NOTLON, *Notropis longirostris*; NOTPET, *Notropis petersoni*; NOTTEX, *Notropis texanus*; OPSEMI, *Opsopoeodus emiliae*; PERNIG, *Percina nigrofasciata*; TRIMAC, *Trinectes maculatus*.

HABITAT VARIATION

Channel habitats varied among tidal river systems longitudinally within systems, as well as across systems, with system size. Upper sites on the Biloxi River, Tuxachanie Creek, and the Tchoutacabouffa River were characteristically more streamlike than channel sites located on lower portions of the systems (Peterson et al., 1995). Channel width varied directly with system size across tidal rivers; habitat conditions and the associated species pool of channels, in turn, influenced pond systems.

Pond sites within a given system usually fell into groups characteristic of small, medium, or large tidal rivers. Exceptions were often due to the proximity of some sites to other large or small systems. For example, the only tidal river pond site within the large-system group that was not within the Pascagoula River was located on lower Bluff Creek near its junction with the Pascagoula River. Conversely, only one Pascagoula pond site fell within the medium-system group, and none from this river system

were associated with the small-system group. Wolf River pond sites were almost equally divided between small- and medium-system groups, with upper Wolf sites being more like small tidal river ponds and lower sites being more like medium tidal river pond sites. Tchoutacabouffa, Biloxi, and Jourdan River pond sites tended to group together as medium-system sites. Small tidal river pond sites typically comprised Bluff Creek and Old Fort Bayou systems.

Habitat conditions of large, medium, and small tidal river pond sites varied according to landscape-scale variation (Table 2). Conductivity and turbidity increased directly with tidal river size. Pond sites from large tidal rivers were physically larger and deeper than those from medium and small tidal rivers. These large ponds were either surrounded and shaded by bald cypress (*Taxodium*) or were large open marsh ponds surrounded by low vegetation (e.g., *Juncus*), including flooded terrestrial vegetation (pers. obs.). Pond sites associated

TABLE 2. Habitat characteristics at the time of sampling for tidal river (TR) side-pond sites. Site affinities determined from groupings in three-dimensional CA space (mean \pm 2 SE) (arcs % = arcsine square root transformed percent) (see Fig. 7).

Habitat characteristic	Small TR pond sites	Medium TR pond sites	Large TR pond sites
Number of sites	23	25	9
Water temperature (C)	26.87 \pm 0.60	27.50 \pm 0.93	29.11 \pm 1.73
Salinity (mg/l)	0	0	0.11 \pm 0.24
Conductivity (μ mho)	61.22 \pm 24.59	140.00 \pm 50.97	166.11 \pm 208.78
pH	5.42 \pm 0.27	6.67 \pm 0.27	6.47 \pm 0.28
Dissolved oxygen (mg/l)	5.65 \pm 0.66	6.34 \pm 0.56	6.08 \pm 1.00
Turbidity (NTU)	10.51 \pm 2.39	14.16 \pm 3.38	18.84 \pm 4.22
Current velocity (m/sec)	0.015 \pm 0.008	0.013 \pm 0.008	0.013 \pm 0.028
Emergent vegetation (arcs %)	51.92 \pm 14.2	19.08 \pm 8.02	34.17 \pm 20.38
Submerged vegetation (arcs %)	74.89 \pm 12.10	68.64 \pm 11.72	15.00 \pm 18.42

with large tidal rivers had much less submerged aquatic vegetation than did pond sites in medium and small tidal river systems, and they also sometimes had traces of salinity.

Landscape-scale habitat features of medium and small tidal rivers were more similar to each other than either was to those of large pond systems. Small tidal river pond sites were characteristically the most acidic, least turbid, least conductive, and most covered by emergent and submerged vegetation (Table 2). Ponds associated with medium and small tidal rivers tended to be surrounded by pine woods (*Pinus*) and were smaller but more variable in size than those of large tidal rivers. Littoral margins of small- and medium-river ponds were more vegetated than those of large tidal rivers, although medium-tidal-river ponds had considerably less emergent vegetation than did small-tidal-river ponds.

DISCUSSION

The biodiversity of littoral tidal river fishes varied meaningfully on several spatial scales. Fish diversity typically appeared to be higher in littoral channel habitats than in side-pond habitats of tidal river systems. Faunal representation by three core groups of littoral fishes, including cyprinids, centrarchids, and fundulids, generally differed between side-pond and channel habitats, and among different tidal river systems. Some of the faunal variation among systems reflected biogeographic (east/west) trends, but most of the variation reflected system-size-related patterns. Among-site similarity in fish assemblage composition reflected both site proximity and system size. Moreover, the degree of variability in assemblage composition corresponded with system size.

By considering various spatial scales of resolution encompassed by multiple drainage systems, we found interesting biodiversity patterns that would not have been apparent from the study of any one drainage or landscape feature (e.g., channel vs side-pond). A combination of hierarchical processes likely influence local assemblage structure, including within-system variation of habitat characteristics. Oberdorff et al. (1995) distinguish local (within site), regional (among sites within a region), and geographical (among regions) perspectives of biodiversity. Understanding of processes at any one scale of organization should help to explain observed patterns at the next higher scale (Wu and Loucks, 1995), whereas processes operating at large spatial scales constrain the expression of local assemblage patterns (Tonn, 1990). Poff and Allan (1995) point out that, "because fish are relatively mobile and long lived, large spatial and temporal scales may be required to adequately describe fish assemblage structure." A better understanding of the organization of fish communities has been reached through studies, like ours, that employ hierarchical perspectives (Tonn, 1990; Tonn et al., 1990; Schlosser, 1991; Oberdorff et al., 1995; Poff and Allan, 1995; Lyons, 1996). As seen in such studies, large-scale factors often found to be important for explaining fish biodiversity patterns include regional considerations of historical and landscape-scale processes.

Although an east/west biogeographic trend in the relative abundance of centrarchids was indicated, regional assemblage patterns were generally most discernible on the landscape scale, rather than through historical coherence. Most members of the three core groups can tolerate the entire range of habitat condi-

tions found throughout the region, yet their composition varied in conjunction with landscape-scale features. In a study of fish communities of Lake Okeechobee, Florida, Chick and McIvor (1994) concluded that littoral fish assemblages similar to those in this study also varied on a landscape scale in conjunction with particular macrophyte species. In our study, large systems were better represented by cyprinids, whereas small and medium-sized systems were better represented by fundulids. Moreover, system size did not correspond with any discernible geographic pattern. Instead, the system size pattern suggested that landscape-level constraints on habitat structure might favor different faunal complements.

In general, sites clustered in CA space in accordance with their degree of physical proximity within any system. However, habitat constraints could also influence assemblage composition. For example, one small pond located in the medium-sized Jourdan River system was grouped with small-system ponds in the CA ordination. In channel habitats, system-size-related variation likely represents differences in species pools among the various tidal rivers and, conversely, similar species pools available for ponds located in close proximity. For example, the distinctiveness of Pascagoula River channel species suggested that system size has a direct bearing on the species pool available for pond assemblage development. Conversely, ponds may provide source areas for nearby channels as well as other ponds, while channel habitats might serve as sink areas for certain species (Pulliam, 1988). Indeed, channel habitats of small river systems had characteristic pondlike assemblages.

Other confounding factors coincident with system size, such as stream-order effects or the degree of estuarine influence, might have obscured or better explained assemblage patterns. For instance, channel sites from the upper Biloxi and Tchoutacabouffa rivers, as well as on Tuxachanie Creek, could have obscured core group patterns, although this longitudinal effect was removed from the CA ordination. Nevertheless, core group profiles from Tuxachanie Creek indicated minimal bias from the inclusion of such streamlike habitats, and the river size effect on core group patterns was not obscured by the inclusion of these sites. Moreover, most of those Tuxachanie Creek sites that were retained within the final channel CA grouped with other small systems, as would be expected based on a system size faunal effect. Other confounding factors that could be confused with system size effects on assemblage

composition include the proximity of sites to estuarine influence and covariation between pond size and system size. Notwithstanding, the small systems of Old Fort Bayou and Bluff Creek had very similar littoral fish assemblages, although they were sampled at different relative distances from the estuary.

In previous studies of fish biodiversity patterns, the influence of landscape-scale factors often dominated even larger scale biogeographic factors (Oberdorff et al., 1995; Poff and Allan, 1995; Lyons, 1996). Historical factors have not been very useful for explaining global patterns of riverine fish diversity (i.e., species richness), while landscape scale (i.e., species area and species energy) factors account for the greatest amounts of global riverine fish diversity (Oberdorff et al., 1995). System-level variations in water temperature and stream gradient predominate regional influences on the organization of fish assemblages in Wisconsin streams (Lyons, 1996), and hydrological variability exerts a strong influence on stream fish assemblage structure across various regions of Wisconsin and Minnesota (Poff and Allan, 1995). Indeed, understanding landscape-scale environmental variation appears to be key to understanding biodiversity patterns of riverine fishes.

This study provides a regional perspective of tidal river fish biodiversity. However, there are several caveats that should be mentioned. First, the data set was not intensive enough to encompass seasonality or multiple riverine habitats. Also, the use of three kinds of collecting gear may have given a biased picture of biodiversity patterns. Consequently, river bottom habitats and large-river species, by definition, were excluded from consideration. Finally, because different sites and systems were sampled during each of the 3 yr, there was the risk of introducing bias from year-to-year hydrological variation. Fortunately, the influence of such hydrological bias in the expression of assemblage patterns was likely minimal owing to near-normal rainfall regimes during all three annual collecting periods.

Despite all these limitations, a comprehensive perspective of regional biodiversity patterns was provided by the large number of collections encompassing the wide range of coastal systems. An improved biogeographic understanding has been gained through the recognition of important landscape-scale factors, such as tidal river size and associated variation in the available species pool. We also noted how local habitat conditions were constrained by landscape-scale processes, such as

those favoring relatively more submerged vegetation, which, in turn, were reflected by the fish assemblage structure. A hierarchical combination of processes must influence local assemblage structure, including variation in system size, the available species pool, and historical factors, as well as within-system variation in pond size, habitat characteristics, and longitudinal effects. Clearly, further work is warranted to test the hypothesis that fish assemblage patterns of Coastal Plain tidal rivers are strongly influenced by landscape-scale processes in connection with variation in drainage size.

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