

FISHES OF THE BAYOU SARA DRAINAGE, LOUISIANA AND MISSISSIPPI,
WITH A DISCRIMINANT FUNCTIONS ANALYSIS OF
FACTORS INFLUENCING SPECIES DISTRIBUTIONJAMES M. GRADY¹, ROBERT C. CASHNER AND JAMES S. ROGERS*University of New Orleans Department of Biological Sciences,
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ABSTRACT

A fish survey of Bayou Sara, a southward flowing tributary to the lower Mississippi River in Mississippi and Louisiana, was conducted between June 1976 and May 1979. Eighty species, representing 17 families are known from the system as a result of survey work in the lower reaches by Louisiana State University, Baton Rouge, and our work in the upper and middle sections of Bayou Sara. Bayou Sara has fewer species than the adjacent Thompson Creek and nearby westward flowing Buffalo Bayou. The species composition is notable in comparison to the other two systems by the absence of common species of petromyzontids, ictalurids and cyprinodontids. Of the families shared by the three drainages, Bayou Sara most closely resembles Thompson Creek.

Distributional data from six permanent collection stations were supplemented with measurements for 17 environmental parameters. The combined data were subjected to a multiple discriminant functions analysis to identify significant environmental variables accounting for the separation of fish distributions. A single discriminant function, principally contributed to by stream position, accounted for 79% of the variance among fish distributions.

INTRODUCTION

The eastern embayment of the lower Mississippi River receives several small to moderate-sized tributaries in southwestern Mississippi and southeastern Louisiana. The major westward flowing tributaries are Big Black River, Bayou Pierre, Coles Creek, and Homochitto and Buffalo rivers. The lowermost tributaries are Tunica Bayou, Bayou Sara and Thompson Creek (Fig. 1).

This region of the lower Mississippi River drainage, the tributaries to the Lake Pontchartrain estuary, and the Pearl River drainage have been extensively surveyed by R.D. Suttkus (Tulane University), N.H. Douglas (Northeast Louisiana University), J.V. Conner (Louisiana State University), and their students, on either a regular or sporadic basis for the past 30 years. In addition, intensive fish faunal surveys have been conducted in Thompson Creek (Guillory, 1981, 1982), Buffalo Bayou (Cashner et al., 1976), Tchefuncte River (Saul, 1974) and Amite

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months of the year. Terrestrial vegetation providing stream cover and allochthonous detritus is heaviest in this region of Bayou Sara. A mixed hardwood and coniferous forest with sweetgum (*Liquidambar styraciflua*), basswood (*Tilia sp.*), water oak (*Quercus nigra*), short leaf pine (*Pinus echinata*), and loblolly pine (*P. taeda*) is the dominant community type (Caplenor et al., 1968). Deep cut banks are prevalent in headwater areas where Bayou Sara occupies a narrow channel (0.5-1.0 m) with alternating pools and riffles.

Further downstream, Bayou Sara encounters four or five broad step-like depositional surfaces, the Pleistocene Terraces (Fisk et al., 1938; Fisk, 1944; Murray, 1961). Soft, shifting sand substrates with patches of fine gravel are characteristic of the terrace areas. Current velocity decreases and turbidity increases in this region of alternating sand bottomed runs and pools.

A small portion of lower Bayou Sara cuts through the Recent Mississippi River flood plain (Fisk et al., 1938). This Recent flood plain is separated from the Pleistocene Terraces by the eastern escarpment of the Mississippi River. Here water levels and other environmental conditions reflect the influence of the Mississippi River. The lower reaches are characterized by large accumulations of silt, slight current, and highly turbid waters. Bayou Sara occupies a broad, shallow basin with depths ranging from 15 cm to 1.5 m and widths ranging from 25 to 60 m during periods of low flow in the Mississippi River.

In the extreme headwaters many small tributaries are occasionally intermittent during summer and early fall. The main channel, however, is spring-fed and has permanent flow year round. Water levels along the watercourse fluctuate with the seasonality of rainfall and prevailing conditions in the Mississippi River.

Stream flow is heaviest during winter and spring, which are the usual periods of heavy rainfall (Snows, 1970).

MATERIALS AND METHODS

A. Physico-chemical Analysis

Water quality determinations, physical measurements and fish collections were taken at selected stations along the main channel of Bayou Sara from February, 1978 through March, 1979. Five stations (Stations 1-5 in Fig. 2) were initially selected for monthly physico-chemical measurements. However, time limitations, due to concurrent fish sampling, dictated an alternative sampling procedure. Three stations were visited one month and the remaining two the next. This system was followed for three months, but then modified so that 17 environmental parameters and fish collections were taken at all five stations bi-monthly. Due to high water and flooding, Station 2 became inaccessible after April,

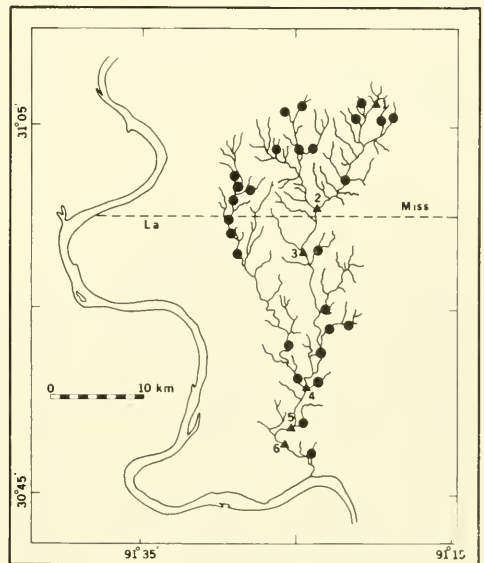


Figure 2. Bayou Sara study area, indicating locations of the 6 permanent stations (triangles) and the 27 supplemental sampling stations (circles).

1978. The close proximity of Station 3 lessened the loss of this sampling site. A downstream site, Station 6, was added in December, 1978.

Conductivity, dissolved oxygen, and water temperature were measured in the field with a YSI Model 33 S-C-T Meter and a YSI Model 51B Oxygen Meter. Additional field measurements included the titrimetric determination of free carbon dioxide and alkalinity, and the colorimetric measurement of pH utilizing a Rascher and Betzold Colorimetric kit. The remaining chemical analyses, turbidity, suspended solids, and total solids, were conducted in the laboratory. Turbidity measurements were made with a Hellige Turbidimeter and evaporation and ashing techniques were used for total and suspended solids determinations.

U.S. Geological Survey topographic maps (1:24,000) were used to determine stream position, stream order, gradient and altitude. Stream order was calculated according to Horton's (1945) method as modified by Strahler (1957). Measurements of mean depth, mean width and current velocity were made according to Lagler (1956). Cross-sectional area was computed following Sobczak (1976).

B. Fish Collections

A survey of the Bayou Sara system was begun in June, 1977 and continued until December, 1977. Fish collections were made concurrently with physico-chemical measurements at five or six of the permanent stations from February, 1978 to March, 1979. Supplemental collections, in addition to those made in 1977, were made at localities throughout the

Bayou Sara system to establish as complete a faunal list as possible. Collection sites are shown in Fig. 3. Fishes were collected with 3.3 m, 4.8 mm nylon mesh seines and originally preserved in 10% formalin.

C. Data Analysis

A multiple discriminant functions analysis subroutine of Nie et al. (1975) was employed to identify environmental parameters contributing to the spatial separation of species. The value of this technique was discussed by Green (1971). Both direct and stepwise methods of discriminant analysis were utilized in this study. The direct method enters all of the independent variables into the analysis concurrently. The discriminant functions are then fitted directly from the entire set of variables. Stepwise discriminant functions analysis permits the exclusion of variables containing little information. Environmental variables are selected for inclusion into the analysis on the basis of their discriminating power. The criterion for establishing discriminating power in this analysis was Rao's V, a generalized distance measure. Those variables which contributed to the largest increase in V, when added to the previous variables, were selected.

Forty-three groups representing the 43 species collected at the permanent stations were designated for input into the analysis. Mean discriminant scores were generated for each of these groups based on the seventeen parameters (13 field and lab measurements plus 4 stream features calculated from topographic maps) measured at the time each species was

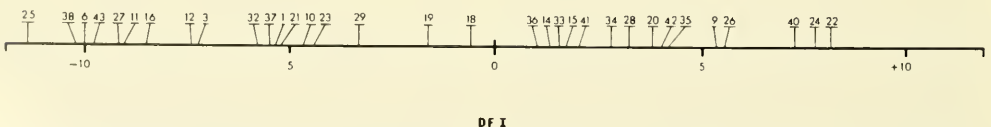


Figure 3. Mean discriminant scores for the first discriminant function (DF I) of the stepwise analysis.

captured.

Several modifications were introduced following the initial analysis. A minimum inclusion level for each group was established following Green (1971). Only those species present in at least two collections at permanent stations were included in subsequent analyses, thereby reducing the number of groups to 33. Because a uniform sampling technique was not employed at each site for the collection of fish, data sets were not weighted by species abundance.

RESULTS

A. Physico-chemical Analysis

Means, ranges and standard deviations of thirteen of the physical and chemical measurements from each of the six stations are presented in Table 1. Because stream position, gradient, altitude and stream order are relatively static, only the observed values are presented in Table 2.

B. Distribution of Fishes

A total of 42,867 specimens was taken in 65 collections at 33 localities in the Bayou Sara system (Fig. 2). Forty-three species, representing 13 families and 27 genera, were collected during the two year study and records for nine more species were obtained from Douglas (1974) and from collection records at the Tulane Museum of Natural History. John Van Conner kindly provided records of an additional 28 species taken primarily in the lower part of the system during surveys by personnel in the Department of Fisheries, Louisiana State University, Baton Rouge. These records include four species represented only by larvae and at least eight species that could potentially range into the main portion of our study area. A complete list of all 80 species from 17 families documented from the Bayou Sara system is presented in Table 3. Nomenclature given follows

Robins et al. (1980).

C. Data Analysis

A maximum of 17 discriminant functions (DF) was extracted during the direct analysis, five of which accounted for 70% of the among-species variance (Table 4). Standardized DF coefficients for the 17 environmental variables for these five DF are also presented in Table 4. The magnitude of the coefficients indicates the relative contribution of each variable to the formation of the DF. Thus altitude and stream position provided the major contributions toward the separation of groups in DF I, which accounted for slightly over 30% of the among-species variance. These two physical parameters remained the most significant factors contributing to the overall separation of the groups (species) in the remaining 16 DF. Total solids and stream order were the only other variables contributing to group separation in all of the 17 DF. Comparisons of the magnitude of the DF coefficients for these parameters, with those for altitude and stream position, reveal, however, that their contributions are only minor. None of the DF extracted during the direct analysis reached a high degree of statistical significance ($p > .05$).

The distributional data and associated environmental parameters were also subjected to a stepwise DF analysis. Two variables, water temperature and stream position, were selected for inclusion into the analysis based on their discriminating power as indicated by a significant increase in Rao's V (Table 5). Discriminant function I accounted for almost 79% of the among-species variance and was significant ($p < .01$). The analysis weighted most heavily on stream position. Although DF II accounted for over 21% of the among-species variance, it failed to attain as high a degree of significance ($p > .05$).

TABLE 1. Means, Ranges, and Standard Deviations of 13 Physico-Chemical Parameters at the 6 Permanent Stations in Bayou Sara

Station	Total Alkalinity (mg/l)	Free CO ₂ (mg/l) ^c	pH	Conductivity (mhos/cm ²)	Total Solids (mg/l)	Suspended Solids (mg/l)	Turbidity (mg/l)
1	35 ^a	9.00	7.01	75	91.04	24.45	2.63
	20 ^b	7.14	0.16	61	87.80	25.39	4.77
	14-72 ^c	1.60-22.0	6.80-7.30	20-215	28.15-293.46	1.31-60.11	0.00-14.00
2	37	1.40	7.13	53	48.65	14.35	0.33
	29	0.17	0.06	5	28.29	1.80	0.29
	20-71	1.20-1.50	7.10-7.20	50-59	32.30-81.32	13.31-16.43	0.00-0.50
3	53	1.19	8.03	82	74.41	29.17	2.84
	21	1.58	0.55	26	36.52	40.57	4.38
	22-78	0.00-3.50	7.00-8.60	40-117	42.23-148.52	3.31-103.31	0.00-11.70
4	46	5.70	7.33	95	180.29	90.30	17.91
	16	5.05	0.16	40	180.40	123.10	17.91
	28-68	0.00-10.90	7.00-7.50	40-180	60.00-582.10	7.50-362.45	0.30-55.30
5	43	8.93	7.28	98	84.27	18.09	5.55
	11	7.86	0.15	27	11.76	24.58	5.87
	33-60	2.40-23.90	7.10-7.50	71-143	66.66-94.72	3.37-67.42	0.00-12.40
6	59	11.25	7.50	91	92.84	28.34	0.20
	13	1.77	0.14	1	17.81	26.64	0.28
	50-68	10.00-12.50	7.40-7.60	90-92	80.25-105.43	9.50-47.18	0.00-0.40

a-mean; b-standard deviation; c-range

DISCUSSION

A. Physico-chemical Factors

Progressional changes in the 17 environmental parameters are evident in Table 1. Values for pH, alkalinity, conductivity, total and suspended solids, turbidity, temperature, mean depth, mean width and cross-sectional area increase downstream. These successively higher values can be attributed to the expected reduction of current velocity and greater accumulations of allocthonous material. Additionally, the progressive downstream rise in temperature is also influenced by the predominance of sand substrates and a reduction of cover associated with reduced riparian vegetation.

Spatial differences in some of the variables can be attributed to the influence of localized conditions. High levels of free CO₂ and correspondingly lower pH values at Station 1 are due in part to increased

deposition of organic material deposited in this area. Turbidity, conductivity, and dissolved and suspended solids at Station 1 were relatively high for an upstream location. Heavy detrital input partially accounts for these high values, but a fallen tree dam acted to further increase the readings. The obstruction also caused higher values for mean depth and width, and cross-sectional area, while decreasing flow rates.

Localized conditions also caused high readings for turbidity, suspended and total solids, and conductivity at Station 4, where a gravel washing operation dramatically increased the suspended particulate matter. At Station 3 the possible presence of lime deposits upstream could explain the consistently high pH and low CO₂ values.

Overall, the deviations from the observed progressional trends from stations 2-6 are probably the result of reduced sampling effort. Still, despite the influence of

TABLE 1 CONT.

Dissolved Oxygen (mg/l)	Temperature (°C)	Current (m/sec)	Mean Depth (m)	Mean Width (m)	Cross-sectional Area (m ²)
9.73	18.86	0.38	0.13	5.49	0.72
2.62	7.26	0.27	0.07	1.13	0.41
7.20-14.40	10.20-28.00	0.12-0.77	0.07-0.27	3.53-6.82	0.3-1.59
13.23	14.27	0.21	0.10	11.80	1.19
0.95	7.39	0.09	0.01	2.69	0.35
12.50-14.30	10.00-22.80	0.16-0.31	0.10-0.11	10.25-14.90	0.99-1.60
9.89	20.63	0.60	0.15	22.98	3.56
1.76	8.75	0.34	0.04	7.39	1.46
7.70-12.10	10.30-29.50	0.18-1.23	0.11-0.20	7.73-31.25	0.91-5.10
8.51	26.76	0.24	0.34	23.98	8.26
2.18	11.58	0.16	0.11	10.15	5.74
6.50-11.50	10.10-37.80	0.14-0.55	0.18-0.45	17.63-46.15	4.05-20.94
8.75	27.15	0.27	0.24	32.00	7.34
1.48	7.75	0.10	0.09	7.10	2.54
7.70-10.80	14.40-34.00	0.16-0.42	0.12-0.32	23.50-40.50	3.97-10.31
9.45	19.75	0.44	0.12	32.82	3.98
1.77	6.72	0.06	0.03	0.78	1.20
8.20-10.70	15.00-24.50	0.39-0.48	0.10-0.14	32.27-33.37	3.13-4.82

localized conditions and sampling error, measurements for the 17 variables fall within the ranges for those reported from comparable stations in adjacent Buffalo Bayou (Rogers et al., 1976) and Thompson Creek (Guillory, 1974).

B. Fish Distributions

Intersystem Distribution. Bayou Sara, like Thompson Creek, has a more depauperate fauna than the larger, westward flowing tributaries to the eastern Mississippi Embayment and adjacent Lake Pontchartrain

TABLE 2. Stream Position, Gradient, Altitude, and Stream Order at Six Physico-Chemical Stations.

Station	Stream Position (km)	Gradient (m/km)	Altitude (m)	Stream Order
1	59.29	5.33	79.26	3.00
2	42.00	1.54	54.86	4.00
3	36.35	1.54	42.67	5.00
4	16.29	0.76	18.29	5.00
5	10.50	0.76	12.19	5.00
6	7.93	1.14	9.14	5.00

TABLE 3. List of Species known to occur in Bayou Sara Drainage, Mississippi and Louisiana. (X= collected during present study; 0= record from Douglas, 1974; TU= Tulane University Museum of Natural History Record; L= LSU record; *= likely to occur in study area).

SPECIES	SOURCE
LEPISOSTEIDAE	
<u>Lepisosteus oculatus</u> - spotted gar	X
<u>Lepisosteus osseus</u> * - longnose gar	L
<u>Lepisosteus platostomus</u> - shortnose gar	X
AMIIDAE	
<u>Amia calva</u> - bowfin	L
ANGUILLIDAE	
<u>Anguilla rostrata</u> * - American eel	TU
CLUPEIDAE	
<u>Alosa chrysochloris</u> * - skipjack herring	L
<u>Dorosoma cepedianum</u> - gizzard shad	X
<u>Dorosoma petenense</u> - threadfin shad	X
HIODONTIDAE	
<u>Hiodon alosoides</u> - goldeye	L
ESOCIDAE	
<u>Esox americanus</u> - grass pickerel	L
CYPRINIDAE	
<u>Cyprinus carpio</u> - common carp	X
<u>Hybognathus hayi</u> - cypress minnow	D
<u>Hybognathus nuchalis</u> - Mississippi silvery minnow	X
<u>Hybopsis aestivalis</u> - speckled chub	X
<u>Nocomis leptocephalus</u> - bluehead chub	X
<u>Notemigonus crysoleucas</u> - golden shiner	X
<u>Notropis atherinoides</u> - emerald shiner	X
<u>Notropis blennius</u> - river shiner	X
<u>Notropis buechanani</u> - ghost shiner	L
<u>Notropis camurus</u> - bluntface shiner	X
<u>Notropis chrysocephalus</u> - striped shiner	X
<u>Notropis emilae</u> - pugnose minnow	TU
<u>Notropis fumeus</u> - ribbon shiner	TU
<u>Notropis longirostris</u> - longnose shiner	X
<u>Notropis lutrensis</u> - red shiner	X
<u>Notropis shumardi</u> * - silverband shiner	L
<u>Notropis texanus</u> - weed shiner	TU
<u>Notropis umbratilis</u> - redbfin shiner	X
<u>Notropis venustus</u> - blacktail shiner	X
<u>Notropis volucellus</u> - mimic shiner	X
<u>Pimephales notatus</u> - bluntnose minnow	X
<u>Pimephales vigilax</u> - bullhead minnow	X
<u>Semotilus atromaculatus</u> - creek chub	X
CATOSTOMIDAE	
<u>Carpiodes carpio</u> - river carpsucker	X
<u>Cycleptus elongatus</u> - blue sucker (larvae only)	L
<u>Erimyzon oblongus</u> - creek chubsucker	X
<u>Erimyzon sucetta</u> - lake chubsucker (larvae only)	L
<u>Hypentelium nigricans</u> * - northern hogsucker	L
<u>Ictiobus bubalus</u> - smallmouth buffalo	X
<u>Ictiobus cyprinellus</u> - bigmouth buffalo	L
<u>Minytrema melanops</u> - spotted sucker (larvae only)	L

TABLE 3. CONT.

SPECIES	SOURCE
ICTALURIDAE	
<u>Ictalurus furcatus</u> - blue catfish	L
<u>Ictalurus melas</u> - black bullhead	L
<u>Ictalurus natalis</u> - yellow bullhead	X
<u>Ictalurus punctatus</u> - channel catfish	X
<u>Pylodictus olivaris</u> - flathead catfish	L
APHREDODERIDAE	
<u>Aphredoderus sayanus</u> * - pirate perch	L
CYPRINODONTIDAE	
<u>Fundulus olivaceus</u> - blackspotted topminnow	X
POECILIIDAE	
<u>Gambusia affinis</u> - mosquitofish	X
<u>Poecilia latipinna</u> - sailfin molly	L
ATHERINIDAE	
<u>Labidesthes sicculus</u> - brook silverside	X
<u>Menidia beryllina</u> * - inland silverside	L
PERCICHTHYIDAE	
<u>Morone chrysops</u> - white bass	X
<u>Morone mississippiensis</u> - yellow bass	L
CENTRARCHIDAE	
<u>Centrarchus macropterus</u> - flier	L
<u>Elassoma zonatum</u> - banded pygmy sunfish	X
<u>Lepomis cyanellus</u> - green sunfish	X
<u>Lepomis gulosus</u> - warmouth	TU
<u>Lepomis humilis</u> - orangespotted sunfish	TU
<u>Lepomis macrochirus</u> - bluegill	X
<u>Lepomis marginatus</u> - dollar sunfish	L
<u>Lepomis megalotis</u> - longear sunfish	X
<u>Lepomis microlophus</u> - redear sunfish	L
<u>Lepomis punctatus</u> - spotted sunfish	L
<u>Lepomis symmetricus</u> - bantam sunfish	L
<u>Micropterus punctulatus</u> - spotted bass	X
<u>Micropterus salmoides</u> - largemouth bass	X
<u>Pomoxis annularis</u> - white crappie	X
<u>Pomoxis nigromaculatus</u> - black crappie	X
PERCIDAE	
<u>Etheostoma asprigene</u> - mud darter	L
<u>Etheostoma caeruleum</u> - rainbow darter	X
<u>Etheostoma chlorosomum</u> * - bluntnose darter	L
<u>Etheostoma gracile</u> - slough darter	D
<u>Etheostoma parvipinne</u> - goldstripe darter	D
<u>Etheostoma proeliare</u> * - cypress darter	L
<u>Etheostoma whipplei</u> - redfin darter	X
<u>Percina ouachitae</u> - saddleback darter	X
<u>Stizostedion canadense</u> - sauger (larvae only)	L
SCIAENIDAE	
<u>Aplodinotus grunniens</u> - freshwater drum	X

drainages (Guillory, 1981). Unfortunately, there is little published on the ichthyofauna of the streams in this region, except for Douglas (1974), Guillory (1981, 1982) and several Master's and Doctoral theses (Saul,

1974; Sobczak, 1976; Laiche, 1980). The number of species known from the two southward flowing lower Mississippi River tributaries, Thompson Creek and Bayou Sara, is similar with 89 and 80, respectively

TABLE 4. Standardized Discriminant Function Coefficients

	FUNC 1	FUNC 2	FUNC 3	FUNC 4	FUNC 5
pH	-0.07780	0.39875	-0.72813	-0.28597	0.97805
D.O.	-0.15755	-0.32399	0.25823	-0.60156	-1.09422
ALKALINITY	-0.06090	-0.16229	0.36258	-0.62893	-0.05940
CONDUCTIVITY	0.25892	0.02589	0.13170	-0.19767	-0.22383
TOTAL SOLIDS	-0.43664	2.09234	0.28884	1.58946	3.10853
SUSP. SOLIDS	0.20762	-0.88644	-0.22385	-0.37946	-1.70610
TURBIDITY	0.17703	-1.60905	-0.02340	-1.76112	-1.07093
FREE CO ₂	0.00197	0.00790	-0.79007	0.14661	-0.08678
DEPTH (M)	0.06194	1.25672	1.09893	-0.73320	0.44940
WIDTH (M)	0.19755	1.39467	-0.35713	-0.84978	1.01854
CURRENT	-0.01765	0.19450	0.35781	-0.67831	0.29226
TEMPERATURE	0.06749	-1.23164	0.13863	-0.43415	-0.18932
CROSS SEC. AREA	0.06456	-1.96236	-0.46527	0.69922	-1.21293
POSITION	-6.56132	51.30540	-38.94077	20.61264	15.37281
ALTITUDE	6.77611	-59.50041	43.58128	-24.48588	-15.89091
GRADIENT	-0.12318	-2.78645	2.82273	1.00519	-3.95386
STREAM ORDER	0.78970	-11.90598	8.33457	-2.24487	-4.94176
Percent of Total Variance Accounted For	30.07	12.21	11.60	8.63	7.33

(Guillory, 1981). Lists for both systems include at least 20 invaders from the Mississippi River and another 4 or 5 species localized in swamps or lower tributaries. Eighty-five species have been documented from Buffalo Bayou, but collecting efforts were concentrated in the upper and middle sections of that system (Cashner et al., 1976; Rogers et al., 1976). We assume that the species total for Buffalo Bayou would be appreciably greater than either Thompson Creek or Bayou Sara if an intensive survey of the lower reaches was conducted.

Bayou Sara is perhaps more noteworthy for the species that do not occur within the system than for those that are recorded. Poor representation of three families, Petromyzontidae, Ictaluridae, and Cyprinodontidae, is the most significant difference between the fauna of Bayou Sara and that of the two adjacent drainages. No lampreys have been taken in Bayou Sara; two species, *Ichthyomyzon gagei* and

Lampetra aepyptera, were reported from Buffalo Bayou and one, *Ichthyomyzon gagei*, from Thompson Creek. A combined total of ten ictalurids, *Ictalurus furcatus*, *I. melas*, *I. natalis*, *I. nebulosus*, *I. punctatus*, *Noturus leptacanthus*, *N. miurus*, *N. nocturnus*, *N. phaeus*, and *Pylodictus olivaris*, has been recorded in Thompson Creek and Buffalo Bayou, with 7 species found in each system. Although 5 catfishes, *Ictalurus furcatus*, *I. melas*, *I. natalis*, *I. punctatus*, and *Pylodictus olivaris* have been collected in Bayou Sara, madtoms (*Noturus*) were notably absent. Three cyprinodontids, *Fundulus catenatus*, *F. notatus*, and *F. olivaceus*, have been taken in Buffalo Bayou and three, *Fundulus chrysotus*, *F. notti*, and *F. olivaceus* have also been reported from Thompson Creek. Only one of these, *Fundulus olivaceus*, was collected in Bayou Sara. In regard to the remaining families that the three drainages share, Bayou Sara is slightly less diverse than either of its two

adjacent drainages with a composition most similar to that of Thompson Creek.

There are several plausible explanations for the lower species diversity in Bayou Sara. Bayou Sara drains an area approximately 495 km², whereas Buffalo Bayou and Thompson Creek each drain more than 800 km². This represents a significantly smaller surface area and, consequently, a smaller volume of water in Bayou Sara. Although there is not a direct correlation between habitat diversity and water volume, an increase in available habitat in terms of both extent and diversity would be expected with larger volumes of water (Hanson and Campbell, 1963; Sheldon, 1968).

Perhaps the two larger systems support more diverse faunas because of increased habitat availability. Thus Bayou Sara may lack suitable habitat or provide only marginal habitat for those species present in Buffalo Bayou and Thompson Creek that it does not share. Additionally, species extinction would be more likely in the smaller Bayou Sara system due in part to the reduction of habitat size associated with smaller volumes of water and correspondingly smaller populations of certain fish species (MacArthur and Wilson, 1967).

Lack of suitable habitat may explain the absence of such species as *Moxostoma poecilurum*, *Noturus phaeus* and *N. nocturnus*, which have been reported from Buffalo Bayou or Thompson Creek (Guillory, 1981). These species are typically associated with firm substrates in contrast

to the shifting sand bottoms characteristic of upper Bayou Sara. Taylor (1969) reported *Noturus phaeus* to be commonly encountered under vegetation in fast flowing streams and that *N. nocturnus* avoids streams with shifting sand bottoms. Paucity of aquatic vegetation, predominance of loose sand substrates, and the absence of moderately deep, swift riffles with firm gravel substrates in Bayou Sara strongly suggest that a number of species are excluded from the system due to lack of suitable habitat.

Habitat requirements alone cannot account for the exclusion from Bayou Sara of several species including *Noturus miurus* and *N. leptacanthus* which appear in adjacent drainages. Taylor (1969) noted that *N. miurus* often occurs in lowland or base level streams with soft substrates and *N. leptacanthus* is common in riffles over sand or gravel substrates. Habitats appropriate for the above species thus appear to be available in Bayou Sara. Therefore, their absence in the system cannot be explained solely on the basis of lack of suitable habitat.

A more complex explanation of Bayou Sara's low species diversity involves environmental changes associated with the geological history of the lower Mississippi River and its tributaries. Primary consideration was given to the effects of Pleistocene glaciation on conditions in the lower Mississippi by Guillory (1978) in a discussion of modes of dispersal of upland species.

TABLE 5. Standardized Discriminant Function Coefficients from Stepwise Analysis.

	FUNC 1	FUNC 2
TEMPERATURE	-0.15230	1.05648
STREAM POSITION	0.93651	0.51216
Percent of Total Variance Accounted For	78.65	21.35

During Pleistocene interglacial periods the lower Mississippi River and associated tributaries experienced an increase in stream load, volume and deposition, followed by periodic inundations by the Gulf of Mexico. Subsequent rejuvenation of these tributary systems occurred in response to sea level lowering during glacial periods (Fisk, 1944). At these times the streams were characterized by lowered baselevels, increased gradients, clearer water and coarser sediments. Guillory (1978) suggested that glacial periods would have presented more favorable conditions for the survival and dispersal of freshwater fishes in the lower Mississippi Valley. Because periods of favorable and unfavorable conditions would have existed in all the major tributaries to the lower southeastern Mississippi River, these events would not account for existing differences in interdrainage species composition.

Recent environmental changes comparable to those mentioned above have been reported by Fisk et al. (1938). Although inundations of the lower Mississippi by the Gulf have not occurred, the meandering of the Mississippi River has produced conditions similar to those during the Pleistocene. Westward movements of the Mississippi bring about a local lengthening of its eastern tributaries, causing an overall decrease in average gradient. Eastward migrations of the river would conversely shorten these tributaries and effectively lower the baselevel. Consequently, tributaries to the eastern embayment experience gradient increases and trench their former floodplains to reach the lower baselevel (Fisk et al., 1938; Guillory, 1976).

Environmental changes associated with decrease in gradient, reduced flow, decreased oxygen tensions, increased temperature and increased siltation may have resulted in marginal, intermittent habitat for many existing species. Local extinction of species would occur if favorable habitat

was not available for survival until reverse migration of the Mississippi River occurred. Guillory (1976) explained the disappearance of the blackbanded darter (*Percina nigrofasciata*) from the Thompson Creek system as a result of such recent changes. The fact that species were eliminated from Bayou Sara and not Buffalo Bayou and Thompson Creek may result from differential retention of favorable habitat during variations in the course of the Mississippi River.

Bayou Sara, Buffalo Bayou and Thompson Creek have relatively steep gradients (Fisk et al., 1938). Steep gradients in Thompson Creek and Bayou Sara result from the localized uplift along the Mobile-Tunica flexure in response to sediment overloading in the Mississippi River delta (Howe, 1936; Fisk et al., 1938). This flexure and the steepest gradient occur along a line through the headwaters of Bayou Sara. A large portion of the upstream sections of Thompson Creek and all of Buffalo Bayou lie above this line. Conceivably, some species survived unfavorable conditions occurring downstream during westward migrations of the Mississippi by moving into higher gradient sections of the tributaries. Only a small portion of the Bayou Sara system shows the high gradient associated with the Mobile-Tunica flexure. Discharge in this area is consistently low and the extreme headwaters become intermittent during dry periods. Sufficient habitat may not have been available for extended periods to support a major influx of downstream species. Therefore, elimination of species could have been more pronounced in Bayou Sara.

Intrasystem Distribution. A pattern of progressive downstream addition of species has been observed in many drainage systems (Thompson and Hunt, 1930; Burton and Odum, 1945; Kuehne, 1962; Hanson and Campbell, 1963; Larimore and Smith, 1963; Harrel et al., 1967; Jenkins and

Freeman, 1972; Whiteside and McNatt, 1972; Lotrich, 1973; Cashner and Brown, 1977; Evans and Noble, 1979; Guillory, 1981). The observed longitudinal distribution of fishes in Bayou Sara (Table 6) does not strictly follow previously described patterns. There is a progressive downstream addition of species from 1-4, reaching a high of 33 at Station 4. However, species number declines further downstream with only 28 species at Station 5 and 21 species at Station 6.

The most abundant components of the headwater fish fauna were *Nocomis leptcephalus*, *Notropis chrysocephalus*, *N. longirostris*, and *Etheostoma caeruleum*. Downstream fauna was characterized by two very abundant cyprinids, *Notropis venustus* and *Pimephales vigilax*, the addition of several species, *Hybognathus nuchalis*, *Notropis atherinoides* and *N. blennioides*, and the presence of *Gambusia affinis*.

Among the 43 species collected during this study, only four, *Nocomis leptcephalus*, *Semotilus atromaculatus*, *Ictalurus natalis* and *Lepomis cyanellus*, were absent from lower reaches of the stream. Nineteen species were restricted to the middle and lower reaches, and 12 are continuously distributed along the main channel or are absent from only a single locality (Table 6).

All 21 species recorded at Station 1 were taken from at least one other locality. Twenty-two species were added from Stations 2-6, four at Station 3, nine at Station 4, three at Station 5 and two at Station 6. Ten species are represented by single specimens.

Variation in discharge and the associated physical and chemical changes may explain, in part, the pattern of longitudinal distribution of fishes in Bayou Sara. Extremely low flow occurred between June and December 1978. Permanent flow did persist at the six stations during this period, but many smaller tributary creeks were intermittent or

dry. Hynes (1972) reported that species survive drought conditions as isolated populations in favored downstream locations, and Larimore et al. (1959) observed that the recolonization of upstream habitats occurred rapidly following restoration of flow.

Downstream displacement of species in response to low water or drought conditions would obscure any tendency for zonation and distort the pattern of species addition. Similar displacement would be expected in small creeks and tributaries to the lower reaches of Bayou Sara. Such downstream shifts may account for the infrequent occurrence of *Erismyzon oblongus*, *Etheostoma caeruleum*, *E. whipplei*, and *Percina ouachitae* at Stations 5 and 6 and *Nocomis leptcephalus*, *Semotilus atromaculatus* and *Ictalurus natalis* at Station 4.

C. Data Analysis

Multiple discriminant functions analysis was employed to assess the importance of 17 environmental variables in regard to spatial separation of the groups (species) in Bayou Sara. Seventeen discriminant functions (DF) were extracted during the direct analysis. Standardized DF coefficients for each of the 17 variables in these functions (Table 4) indicate the dominance of two factors, altitude and stream position.

The high positive coefficient for gradient in DF I, in conjunction with the prominent negative one for stream position, indicates a marked restriction of species to the headwaters and lower reaches of Bayou Sara. According to the analysis, the downstream variation in altitude and stream position accounts for the longitudinal variation in species distribution in the Bayou Sara system. Because, however, the 17 DF extracted during the direct analysis failed to reach a high degree of statistical significance ($p > .10$), sufficient variation between species apparently does not exist in these two variables and the other 15 parameters to account for the observed species separations.

TABLE 6. Longitudinal Distribution of Fishes in Bayou Sara. Line is continuous if a species was not missing from one or more successive localities, otherwise the line is dashed.

STATION	1	2	3	4	5	6
	CODE					
<u>Lepomis cyaneellus</u>	_____	--- --	_____	_____	_____	_____
<u>Ictalurus natalis</u>	_____	_____	_____	_____	_____	_____
<u>Semotilus atromaculatus</u>	_____	_____	_____	_____	_____	_____
<u>Nocomis leptocephalus</u>	_____	_____	_____	_____	_____	_____
<u>Micropterus salmoides</u>	_____	--- --	--- --	--- --	_____	_____
<u>Erimyzon oblongus</u>	_____	--- --	_____	_____	_____	_____
<u>Micropterus punctulatus</u>	_____	--- --	_____	_____	_____	_____
<u>Fundulus olivaceus</u>	_____	_____	_____	_____	_____	_____
<u>Notemigonus crysoleucas</u>	_____	_____	--- --	_____	_____	_____
<u>Etheostoma whipplei</u>	_____	--- --	--- --	--- --	--- --	_____
<u>E. caeruleum</u>	_____	_____	_____	_____	_____	_____
<u>Percina ouachitae</u>	_____	_____	_____	_____	_____	_____
<u>Pimephales notatus</u>	_____	_____	_____	_____	_____	_____
<u>Carpionodes carpio</u>	_____	_____	_____	_____	_____	_____
<u>Notropis chrysocephalus</u>	_____	_____	_____	_____	_____	_____
<u>N. longirostris</u>	_____	_____	_____	_____	_____	_____
<u>N. venustus</u>	_____	_____	_____	_____	_____	_____
<u>N. volucellus</u>	_____	_____	_____	_____	_____	_____
<u>Gambusia affinis</u>	_____	_____	_____	_____	_____	_____

TABLE 6 CONT.

STATION	1	2	3	4	5	6
	CODE					
<u>Lepomis macrochirus</u>	33					
<u>L. megalotis</u>	34					
<u>Pimephales vigilax</u>	21					
<u>Ictalurus punctatus</u>	37					
<u>Notropis lutrensis</u>	16					
<u>Pomoxis annularis</u>	37					
<u>Notropis umbratilis</u>	17					
<u>Lepisosteus oculatus</u>	1					
<u>Dorosoma cepedianum</u>	3					
<u>Ictiobus bubalus</u>	25					
<u>Pomoxis nigromaculatus</u>	38					
<u>Hybognathus nuchalis</u>	6					
<u>Notropis atherinoides</u>	11					
<u>N. blenni</u>	12					
<u>Aplodinotus grunniens</u>	43					
<u>Notropis camurus</u>	13					
<u>Cyprinus carpio</u>	5					
<u>Labidesthes sicculus</u>	30					
<u>Dorosoma petenese</u>	4					
<u>Lepisosteus platostomus</u>	2					
<u>Elassoma zonatum</u>	39					
<u>Morone chrysops</u>	31					
<u>Hybopsis aestivalis</u>	7					
<u>H. storeriana</u>	8					

Similar results were obtained with the stepwise DF analysis, with stream position and temperature selected for inclusion into the analysis. One statistically significant ($p < 0.01$) DF, accounting for 78.7% of the among-species variance, was extracted during the stepwise analysis. As was the case in the direct analysis, stream position provided the most significant contribution to the formulation of this function. The high positive standardized coefficient for this variable (Table 5) indicates once again a distinct separation of species at upstream localities. The negative coefficient for temperature signifies species separation in the cooler waters of the upstream stations. However, the magnitude of the coefficient for temperature indicates a minor contribution to this function.

Discriminant functions scores for each of the 33 species were also computed during the analysis. These scores were based on physical and chemical measurements associated with the time of capture of each species. A discriminant score is thus obtained for a species for each instance it was collected. Mean discriminant scores were tabulated to facilitate evaluation of species distribution in relation to important environmental variables. Large discriminant scores indicate the presence of a species where significant environmental variables of that function are also correspondingly large or small depending on the signs of the DF coefficients (Nie et al., 1975).

Figure 3 is a plot of the mean discriminant scores for 33 species on DF I of the stepwise analysis. The underlined numbers correspond to one of the 43 species collected during this study. A key to the species codes appears in Table 6. The distribution of mean discriminant scores (Fig. 3) appears to corroborate the observed pattern of longitudinal distribution of species in Bayou Sara (Table 6). Three species, *Semotilus atromaculatus* (22), *Erismyzon oblongus*

(23), and *Etheostoma caeruleum* (40), were restricted to upstream areas where water temperatures were the lowest. Although not restricted to the most upstream stations, two species, *Nocomis leptcephalus* (9) and *Ictalurus natalis* (26), appear to have been limited to more upstream localities with cooler water temperatures. A large number of species were either restricted to the mid-stream sections of Bayou Sara or were continuously distributed along the watercourse ($-0.5 < DS < +0.5$). Furthermore, a number of species had their distribution limited to the lower reaches where water temperatures were the highest.

Results of both the direct and stepwise DF analyses are consistent with the findings of Sobczak (1976) and Rogers, et al. (1976). Physical measurements of mean depth, cross-sectional area, stream position and altitude were the most significant environmental factors contributing to separation of species in Bayou Lacombe, Louisiana (Sobczak, 1976). Rogers et al. (1976) found stream depth, width and alkalinity to be the most important factors accounting for variance among intrasystem distributions in Buffalo Bayou, Mississippi.

One reason for the dominance of physical factors in separating species distributions in these two studies and especially Bayou Sara can be postulated. The range of variation within the stream systems, relative to the fishes' ranges of tolerance, may be smaller for the chemical factors than for the physical factors. Physical measurements would therefore, assume more importance in determining the distribution of species that are not adversely affected by the range of chemical conditions encountered in each of these streams.

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LITERATURE CITED

- BAKER, J. A. and S. T. ROSS. 1981. Spatial and temporal resource utilization by southeastern cyprinids. *Copeia* 1981: 178-189.
- BURTON, G. W. and E. P. ODUM. 1945. The distribution of stream fish in the vicinity of Mountain Lake, Virginia. *Ecology* 26:182-194.
- CAPLENOR, C. D., R. E. BELL, J. BROOK, D. CALDWELL, C. HUGHES, A. SCOTT, S. WARE, and M. WELLS. 1968. Forests of west-central Mississippi as affected by loess. In: Loess investigations in Mississippi. Mississippi Geol., Econ. and Topogr. Surv. Bull. 3:205-267.
- CASHNER, R. C. and J. D. BROWN. 1977. Longitudinal distribution of fishes of the Buffalo River in northwestern Arkansas. *Tulane Stud. Zool. and Bot.* 19:37-46.
- _____, J. S. ROGERS and M. T. SOBCZAK. 1976. The fishes of the Buffalo River in western Mississippi. *ASB Bull.* 23:48. Abstract.
- DOUGLAS, N. H. 1974. Freshwater fishes of Louisiana. Claitor's Publ. Div., Baton Rouge, Louisiana.
- EVANS, J. W. and R. L. NOBLE. 1979. The longitudinal distribution of fishes in an east Texas stream. *Am. Midl. Nat.* 101:333-343.
- FISK, H. N. 1944. Geological investigations of alluvial valley of the lower Mississippi River. *Miss. River Comm. Rept.*, 1-78.
- _____, H. G. RICHARDS, C. A. BROWN, and W. C. STEERE. 1938. Contributions to the Pleistocene history of the Florida parishes of Louisiana. Louisiana Dept. Conserv. Geol. Bull. 12:1-137.
- GREEN, R. H. 1971. A multivariate statistical approach to the Hutchinson niche: bivalve molluscs of central Canada. *Ecology* 52:543-556.
- GUILLORY, V. 1974. Distribution and abundance of fishes in Thompson Creek and lower Mississippi River, Louisiana. M.S. thesis, Louisiana State Univ., Baton Rouge. (Unpublished).
- _____. 1976. Apparent absence of *Percina nigrofasciata* from the Mississippi Valley. *Copeia* 1976: 805-806.
- _____. 1978. New interpretations of fish dispersal via the lower Mississippi River. *Florida Scient.* 41:96-100.
- _____. 1981. A checklist of fishes of Thompson Creek, Louisiana, with zoogeographical comments. *Louisiana Acad. Sci.* 44:37-47.
- _____. 1982. Longitudinal gradients of fishes in Thompson Creek, Louisiana. *Southwestern Nat.* 27:107-115.
- _____, and J. V. CONNER. 1973. Fishes of Thompson Creek in the Feliciana parishes of Louisiana and Mississippi. *ASB Bull.* 20:56. Abstract.
- HANSON, W. D. and R. S. CAMPBELL. 1963. The effects of pool size and beaver activity on distribution and abundance of warm-water fishes in a north Minnesota stream. *Am. Midl. Nat.* 69:136-149.
- HARRELL, R. C., B. J. DAVIS, and T. C. DORRIS. 1967. Stream order and species diversity of fishes in an intermittent Oklahoma stream. *Am. Midl. Nat.* 78:428-438.
- HEINS, D. C. and G. H. CLEMMER. 1975. Ecology, foods, and feeding of the longnose shiner, *Notropis longirostris* (Hay), in Mississippi. *Am. Midl. Nat.* 94:284-295.
- HORTON, R. E. 1945. Erosional developments of streams and their drainage basins; hydrophysical approach to quantitative morphology. *Geol. Soc. Am. Bull.* 56:275-370.
- HOWE, H. 1936. Louisiana petroleum stratigraphy. *Am. Petrol. Inst., Pap.* 201-12B:1-27.
- HYNES, H. B. N. 1972. The ecology of running waters. Univ. Toronto Press, Toronto.
- JENKINS, R. E. and C. A. FREEMAN. 1972. Longitudinal distribution and habitat of the fishes of Mason Creek, an upper Roanoke River drainage tributary, Virginia. *Virginia J. Sci.* 23:194-202.
- KUEHNE, R. A. 1962. A classification of streams, illustrated by fish distribution in an eastern Kentucky stream. *Ecology* 43:608-614.
- LAGLER, K. F. 1956. Freshwater fishery biology. W. C. Brown Co., Dubuque, Iowa.
- LAICHE, G. S. 1980. Fishes of the Amite River drainage in Louisiana and Mississippi. M.S. thesis, Univ. New Orleans, New Orleans. (Unpublished).
- LARIMORE, R. W., W. F. CHILDERS, and C. HECKROTTE. 1959. Destruction and re-establishment of stream fish and invertebrates affected by drought. *Trans. Am. Fish. Soc.* 88:261-285.
- LARIMORE, R. W. and P. W. SMITH. 1963. The fishes of Champaign County, Illinois, as affected by 62 years of stream changes. *Bull. Illinois Nat. Hist. Surv.* 28:299-382.

- LOTTRICH, V. A. 1973. Growth, production and community composition of fishes inhabiting a first-, second-, and third-order stream of eastern Kentucky. *Ecol. Monogr.* 43:377-397.
- MACARTHUR, R. H. and E. O. WILSON. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey. 203 p.
- MOYLE, P. and R. NICHOLS. 1973. Ecology of some native and introduced fishes of the Sierra Nevada. *Ecol. Monogr.* 43:377-397.
- MURRAY, G. E. 1961. Geology of the Atlantic and Gulf Coastal Province of North America. Harper and Row, New York, 692 p.
- NIE, N., C. H. HULL, J. G. JENKINS, K. STEINBRENNER and D. H. BENT. 1975. Statistical package for the social sciences, 2nd ed. McGraw-Hill, New York, 686 p.
- ROBINS, C. R., R. M. BAILEY, C. E. BOND, J. R. BROOKER, E. A. LACHNER, R. N. LEA and W. B. SCOTT. 1980. A list of common and scientific names of fishes from the United States and Canada. *Am. Fish. Soc. Spec. Publ.* 12.
- ROGERS, J. S., R. C. CASHNER and M. T. SOBCZAK. 1976. Multivariate analysis of fish distribution patterns in a small stream system. *Am. Zool.* 16:269. Abstract.
- SAUL, G. E. 1974. Ichthyofaunal investigation of the Tickfaw River drainage basin. M.S. thesis. Louisiana State University, Baton Rouge. (Unpublished).
- SHELDON, A. L. 1968. Species diversity and longitudinal succession in stream fishes. *Ecology* 49:193-198.
- SIBLEY, J. H. 1972. A study of the geology of Baton Rouge and surrounding southeast Louisiana area. Claitor's Publ. Div., Baton Rouge, Louisiana.
- SMITH, G. R. and D. R. FISHER. 1970. Factor analysis of distribution patterns of Kansas fishes. *In:* Pleistocene and recent environments of the central Great Plains. Dept. Geol., Univ. Kansas, Special Publ. 3:259-277.
- SMITH, C. L. and C. R. POWELL. 1971. The summer fish communities of Brier Creek, Marshall county, Oklahoma. *Am. Mus. Novitates*. No. 2458. 30 p.
- SNOWS, T. N. 1970. Water resources of Mississippi. Mississippi Geol. Econ. and Topogr. Surv. Jackson, Mississippi.
- SOBCZAK, M. T. 1976. Physical and chemical factors affecting the distribution and occurrence of fishes in Bayou Lacombe, Louisiana. Ph.D. thesis, Tulane Univ., New Orleans. (Unpublished).
- STEVENSON, M. M., G. D. SCHNELL and R. BLACK. 1974. Factor analysis of fish distribution patterns in western and central Oklahoma. *Syst. Zool.* 23:202-218.
- STRAHLER, A. N. 1957. Quantitative analysis of watershed geomorphology. *Am. Geophys. Union Trans.* 38:913-920.
- TAYLOR, W. R. 1969. A revision of the catfish genus *Noturus* Rafinesque, with an analysis of higher groups in Ictaluridae. *Bull. U.S. Natl. Mus.* 282:1-315.
- THOMPSON, D. and F. HUNT. 1930. The fishes of Champaign County. A study of the distribution and abundance of fishes in small streams. *Bull. Illinois Nat. Hist. Surv.* 19:1-101.
- WALLACE, D. C. 1973. The ecology of the silver-jaw minnow, *Ericymba buccata* Cope. *Am. Midl. Nat.* 87:172-190.
- WHITESIDE, B. E. AND R. M. McNATT. 1972. Fish species diversity in relation to stream order and physicochemical conditions in the Plum Creek drainage basin. *Am. Midl. Nat.* 88:90-101.