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Stream Erosion and Densities of *Etheostoma rubrum* (Percidae) and Associated Riffle-Inhabiting Fishes: Biotic Stability in a Variable Habitat

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The Bayou Pierre system in western Mississippi is currently experiencing extensive erosion, with pulses of erosion moving from lower to higher stream reaches (e.g., headcutting). This erosion has caused substantial changes to the system, including channel widening and deepening, general loss of downstream riffle habitats, and the creation of new riffle habitats in more upstream locations. We address the impact of the rapid and ongoing geomorphic changes on *Etheostoma rubrum* [bayou darter; a federally listed species (Threatened) endemic to Bayou Pierre] and associated, riffle-inhabiting species, including *Etheostoma lynceum* (brighteye darter), *Noturus hildebrandi* (least madtom), *Cyprinella camura* (bluntnose shiner), and *Etheostoma whipplei* (redfin darter). We first characterize stream reaches based on geologic and geomorphic data and then estimate population densities of riffle-inhabiting fishes in each geomorphically homogeneous stream reach. To assess trends in relative abundances of all riffle-inhabiting fishes and population sizes of numerically dominant riffle-inhabiting fishes, we compare relative abundances and densities from 1993–1994 with those from 1986–1988. There is an overall trend for recent erosion to occur in the upper reaches of the Bayou Pierre system, with lower reaches characterized by later, recovery, stages. Between 1940 and 1994, the point of active headcutting moved over 7 km upstream at rates of 48–750 m/yr. The relative abundances of *E. rubrum* and associated riffle-inhabiting fishes have not changed significantly from 1986–1994. Combined densities of all riffle-inhabiting fishes, as well as densities of three of the four most abundant species (*E. rubrum*, *E. lynceum*, *N. hildebrandi*), have also remained temporally stable. Overall, densities of riffle-inhabiting fishes averaged $6.7 \pm 0.2/m^2$. The density of all riffle-inhabiting fishes varied across geomorphic stages, as did the densities of *E. rubrum*, *E. lynceum*, and *N. hildebrandi*, with higher fish numbers in areas of active or recent erosion. This has resulted in a general pattern of greater fish densities in more upstream areas. Ultimate factors responsible for the rapid headcutting are located downstream of currently affected reaches in Bayou Pierre and the Mississippi River. These potentially include natural meander cut-offs, channel avulsion, channelization, and instream gravel mining. Thus, river-management decisions impacting areas spatially distant from the study area appear to have resulted in major local changes.

HABITAT provides the foundation upon which the biological processes of organisms, populations, and communities occur. As pointed out by Southwood (1977) and others, habitats must be considered in terms of their heterogeneity in time and space, and habitat fragmentation (both temporal and spatial) directly affects habitat suitability for the biological community. Habitats are in turn embedded within larger areas and can be affected by changes in landscape patterns (Schlosser, 1991; Grossman et al., 1995).

Numerous studies have addressed the role of habitat in structuring stream fish assemblages (e.g., Sheldon, 1967; Taylor, 1997), and such assemblages are often separated along pool (depositional)-riffle (erosional) gradients (Gelwick, 1990). Changes in lotic habitats resulting from

human impacts are widespread, and ultimate causes of local habitat changes may occur elsewhere in the broader landscape (e.g., Patrick et al., 1982; Smith and Patrick, 1991). Sedimentation, resulting from bank and channel erosion, is particularly pervasive and can alter densities of benthic, riffle-inhabiting insectivorous and herbivorous fishes (Berkman and Rabeni, 1987).

Various studies have examined long-term variation in assemblage structure (e.g., Ross et al., 1987) and microhabitat use (e.g., Grossman and Ratajczak, 1998; Grossman et al., 1998) of stream fishes under conditions of varying flow regimes. Grossman et al. (1995) also quantified substratum variability and discussed implications of such variability on benthic stream fishes. However, few studies have examined the

long-term impacts of major variation in channel geomorphology on assemblage structure and population densities of southeastern stream fish assemblages.

The Bayou Pierre system in western Mississippi is undergoing extensive erosion (Patrick et al., 1991; Ross et al., 1992; Albertson and Patrick, 1996) and thus exposes stream fishes to spatial and temporal habitat variation. Previous investigations using aerial imagery and field observations have shown that the middle and upper reaches of this system, in particular, have experienced accelerated erosion produced by rapid headcutting (Patrick et al., 1991; S. T. Ross, D. M. Patrick, M. T. O'Connell, and C. A. Latorre, 1995, unpubl.).

Headcutting, the upstream migration of a knickpoint (a point of a major change in stream gradient; Mount, 1995), can be caused by downstream channelization or changes in meander belts that produce steeper channel gradients and result in increased water velocities and erosion. These erosional processes alter channel cross-sectional geometry by deepening and widening the channel, resulting in the loss of riparian vegetation caused by bank failure, and causing changes in sediment characteristics in the vicinity of the knickpoint (Schumm et al., 1984). The migration of a knickpoint through a channel reach may cause the loss of riffle habitat downstream through sedimentation, as well as create new riffle areas upstream; however, the net change in suitable habitat for specific riffle-inhabiting fishes, such as *E. rubrum*, and the impact on population densities of these fishes are not known.

The bayou darter, *Etheostoma (Nothonotus) rubrum*, is endemic to the Bayou Pierre system in western Mississippi (Raney and Suttkus, 1966; Ross et al., 1992). Because of its limited natural range, and especially because of the ongoing habitat change in Bayou Pierre and its tributaries, *E. rubrum* is listed as "threatened" under the Endangered Species Act (USFWS, 1990) and listed as "endangered" by the state of Mississippi (Mississippi Natural Heritage Program, 1998, unpubl.).

Individuals of *E. rubrum* are extremely habitat specific (Ross et al., 1990, 1992), occurring in microhabitats typified by swift (mean = 79 cm/sec), shallow water, flowing over a firm, coarse gravel substratum (mean particle size = 16–32 mm). In a laboratory study of substrata preferences (Ross et al., 1992), *E. rubrum* chose a larger substratum (pebbles, 32–64 mm), when compared to the field data, suggesting that suitable riffle habitats (e.g., those with pebbles) might be in limited supply. Sediment generated by

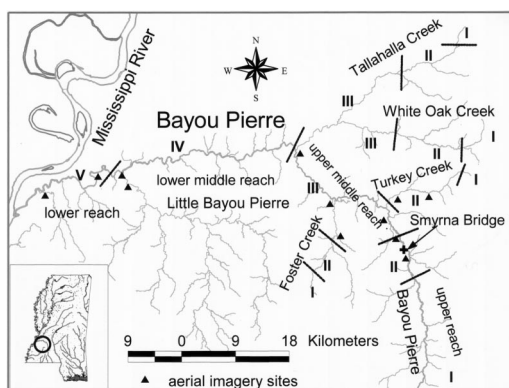


FIG. 1. The Bayou Pierre system in southwestern Mississippi showing place names, locations of aerial imagery data, and geomorphic stages (roman numerals). Geomorphic stages are only mapped on major tributaries.

erosion may cover gravel and pebble-bottomed riffles and thus reduce habitat available to *E. rubrum* and other riffle-inhabiting fishes.

In this study, we first characterize individual reaches of Bayou Pierre and its tributaries in terms of similar geologic and geomorphic conditions. We then determine the response of *E. rubrum* and other riffle-inhabiting fishes to these physical conditions. Specifically, we address the following questions: (1) Has the assemblage structure of riffle-inhabiting fishes changed over time? (2) Have densities of *E. rubrum* and other riffle-inhabiting fishes changed over time? (3) Has the spatial distribution of *E. rubrum* changed as headcutting has moved upstream? and (4) Do growth patterns of *E. rubrum* vary relative to geomorphic conditions?

MATERIALS AND METHODS

Stream system.—Bayou Pierre is a fifth order stream (stream order follows Horton, 1945; as modified by Strahler, 1957) that joins the Mississippi River in Mississippi. Riffle habitats in Bayou Pierre are formed primarily from graveliferous deposits derived from the Plio-Pleistocene Citronelle Formation, which caps the upland areas of the watershed, and by erosion-resistant strata of the Miocene Catahoula Formation (Albertson and Patrick, 1996). We designated four major reaches within the Bayou Pierre system (Fig. 1): (1) upper reach, headwaters to just upstream of the Smyrna bridge; (2) upper middle reach, Smyrna bridge to White Oak Creek; (3) lower middle reach, White Oak Creek to Little Bayou Pierre; (4) lower reach, mouth of Little Bayou Pierre to the Mississippi River.

TABLE 1. THE NUMBER OF ENCLOSURE AND NONENCLOSURE RIFFLE SAMPLES FROM FOUR GEOMORPHIC STAGES OF THE BAYOU PIERRE SYSTEM, 1993–1994.

Geomorphic stage	Bayou Pierre enclosure		Foster Creek enclosure		Turkey Creek enclosure	
	Yes	No	yes	no	yes	no
I	3	1	—	3	—	3
II	9	1	9	—	5	—
III	9	—	9	—	6	—
IV	6	1	—	—	—	—
Total	27	3	18	3	11	3

Geomorphic characterization.—The occurrence of recent erosion was determined by field observations and by analysis of U.S. Department of Agriculture aerial imagery (for 1940, 1950, 1964, 1978, 1985, and 1991 or 1992; locations of aerial images shown on Fig. 1). Erosional stages were classified based on a modification of Schumm et al. (1984), who developed a five-stage classification for reaches of streams that had undergone headward erosion (headcutting). As headcutting proceeds upstream, reaches of the stream pass through these five stages: I—the natural channel prior to headcutting; II—channel deepening has recently started, channel width is increasing through erosion, the banks are becoming steeper than stage I, and there may be loss of bank-line vegetation; III—the stream has become wider and deeper, the banks are quite steep but have not yet failed, and there may be loss of bank-line vegetation; IV—banks have failed, trees have fallen into the stream, the stream appears much wider as a result of the failed banks, there is much sediment in the channel and, at low water stages, the stream may appear to be braided; V—erosional processes have essentially ceased, the stream is no longer braided but is often meandering, point bars have become more-or-less stable, and the upper portions of the point bars have become revegetated. The stage V-stream is meandering upon a new floodplain that may be significantly lower in elevation than the old one that is now a terrace.

Fish sampling, 1986–1988.—Summer (July to September) population densities of riffle-inhabiting fishes were estimated each year from 9–16 sites, chosen randomly from all sites from which *E. rubrum* had been previously collected (based on S. T. Ross, D. M. Patrick, M. T. O'Connell, and C. A. Latorre, 1995, unpubl.). The selection process was constrained by the qualification that no more than one riffle was sampled from a 100–200-m section of stream. Sample sites were stratified by water body, with approximately

twice as many sites chosen from Bayou Pierre as from Foster Creek; two sites were chosen from Turkey Creek.

Fish sampling, 1993–1994.—We sampled from October to November in 1993 and from May to October in 1994 (43 of 50 samples were taken from July to September). The length of stream in erosional stages I–IV (stage V occurred only in the lower reach of Bayou Pierre where riffles are uncommon) was divided into 1-km reaches; then three reaches were randomly chosen in each erosional stage. Randomization was not stratified between 1993 and 1994 so that these samples are treated together (referred to in analyses as 1994).

For each 1-km reach, the total number of riffles present was determined in the field by walking the stream section. Three of these riffles were randomly chosen as areas for population estimates of the fish assemblage. If no suitable habitat sites (i.e., riffles) were present, we verified the absence of *E. rubrum* by thoroughly sampling any shallow, flowing areas with a 10' seine (= nonenclosure sample). Overall, we sampled 30 riffles in Bayou Pierre, 21 in Foster Creek, and 14 in Turkey Creek, of which 27, 18, and 11, respectively, were enclosure population estimates (Table 1). Thus, population estimates are for areas of riffle habitats and are not estimates of average fish density over all stream habitats (e.g., pools, runs, and riffles).

Population density.—At each site, steel poles were driven into the riffle to enclose a 12.5-m² area (enclosed areas were smaller if riffles had a total area of less than 12.5 m²). After a 20–25-min wait, we enclosed the poles with 3.2-mm (1/8") nylon Ace netting and secured the netting to the stream bottom with steel rods and rocks. It usually required 2–4 min to enclose a riffle. We removed fishes from the enclosed riffle by four sets of standardized seine hauls, with each haul covering an area of 1.25 × 2.5 m and beginning at the upstream end of the enclosure. Each sub-

sequent haul was approximately 1.25 m further downstream until the lower end of the enclosure was reached. Four seine hauls comprised one set, and the process was repeated for a total of four sets. In 1986, seine hauls were taken until three consecutive hauls did not yield any fishes. For analysis, these hauls were grouped into sets of four, as described above, except that the number of sets varied from 3–7.

During each haul the area being seined was vigorously kicked to drive fishes into the net. We estimated densities and variances using a maximum likelihood estimator (Cowx, 1983; T. J. Kwak, 1991, unpubl.; Kwak, 1992). In addition to *E. rubrum* (which were released), densities were also determined for all other commonly occurring fishes. These fishes were fixed in the field in 10% formalin and returned to the laboratory for identification. All of these fishes are archived in the University of Southern Mississippi (USM) Museum of Ichthyology.

Statistical analyses of spatial, temporal, and geomorphic trends.—In 1986–1988, sites for population estimates were randomly chosen from a list of all known bayou darter sites, whereas in 1993–1994, we randomly selected riffles, without the constraint that *E. rubrum* previously had been collected there. Thus, to jointly compare species composition among years, or density of fishes among years and streams, we only used data from population enclosures in which *E. rubrum* were also present. Because more enclosures were sampled in 1993–1994 than in the previous years, we adjusted sample sizes for the temporal comparisons by determining the maximum number of enclosures sampled per year from 1986–1988 (Bayou Pierre = 9; Foster Creek = 5; Turkey Creek = 1) and by randomly selecting that number of samples from each stream from the 1993–1994 data. White Oak Creek was not included in the 1993–1994 dataset; thus, it is omitted from the analysis of spatial or temporal changes.

We tested for stability of the riffle-fish assemblage among years with rank concordance statistics (Kendall's W). Tests were corrected for ties and significance was determined following Daniel (1978). Because our interest was in stability of the numerically dominant species, rather than all species potentially occurring in the riffle habitats, we excluded species not comprising at least 1% of the total fish collected in at least one year.

We used two-way analysis of variance to determine whether there were significant interactions among years and streams in the density of all riffle-inhabiting fishes, or in the density of *E.*

rubrum. Densities were log-transformed [$\ln(\text{density} + 1)$], which eliminated heteroscedasticity. However, because this was based on a more restrictive dataset (total number of fishes, or only *E. rubrum*, and Bayou Pierre and Foster Creek only), we also analyzed for temporal and spatial trends separately using one-way analysis of variance, again checking for normality and homogeneity of variances. Posthoc comparisons were made using the Scheffe Test ($\alpha = 0.05$). If variances were not homogenous, we used the nonparametric Kruskal-Wallis test. We used a sequential Bonferroni method to yield a table-wide significance level (Holm, 1979; Sokal and Rohlf, 1995) when multiple comparisons were made from a single dataset.

Variation in the density of fishes among erosional stages was examined in two ways using the combined 1993–1994 data (data on geomorphic stages were not taken prior to 1993). First, based on enclosure data, we used a two-way ANOVA of geomorphic stages II and III and water body to test the null hypothesis of no variation in density among stage or water body. This analysis was restricted to total fish density and to the density of *E. lynceum* (the only two groups having homogeneous variances). Second, we used the nonparametric Kruskal-Wallis test to evaluate the hypothesis of no variation in total riffle fish density and the density of dominant species among the four erosional stages for Bayou Pierre only (*E. rubrum* were not collected in erosional stages I and II of either Foster or Turkey Creeks, and no stage-IV habitat was identified in these streams). Except where noted, statistical tests were done using SPSS (SPSSX 2.1, 1986, unpubl.; SPSS 9.0 for Windows, 1999, unpubl.).

Length-mass relationships.—For all *E. rubrum* captured during 1993–1994 population estimates, we determined standard length (SL, to the nearest 0.1 mm) and mass in water (to 0.01 g using a portable electronic balance). Mature fish were sexed using external characteristics (i.e., color pattern and body shape). Fish were lightly anesthetized with tricaine methanesulfonate (MS-222) prior to measuring, following techniques of Stickney (1983). Following measurement, we placed the fish in a bucket of stream water until they showed active swimming behavior, after which they were released at the point of original collection. Condition of *E. rubrum*, based on mass-length relationships, was compared using ANCOVA (program PIV, BMDP, 1985, unpubl.). Data were rank-transformed (RT2) prior to analyses following Conover and Iman (1981). We used predictive rath-

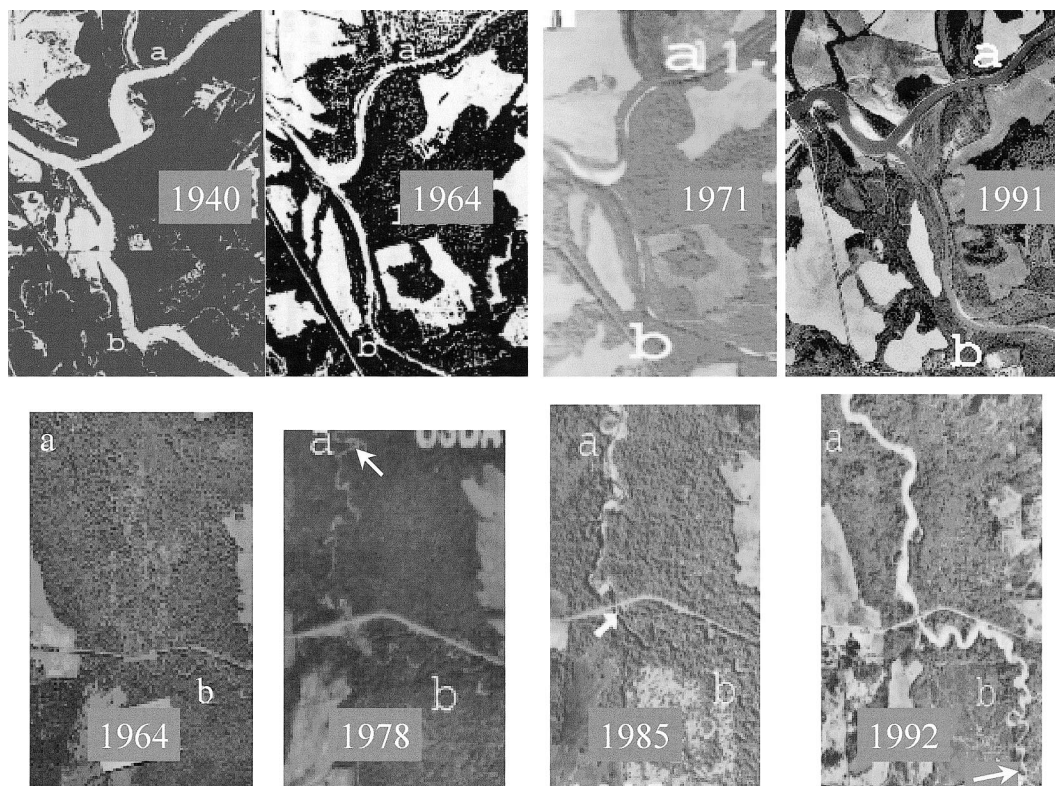


FIG. 2. Upper four panels: aerial imagery site I-3 located on the lower reach of Bayou Pierre at the confluence with little Bayou Pierre. Lower four panels: aerial imagery site I-12 located on the upper reach of Bayou Pierre in the vicinity of the Smyrna bridge. Common points in each frame are indicated by "a" and "b"; arrows show knickpoints.

er than functional regressions, as recommended by Cone (1989). Only age-1 fish (determined from visual examination of length-frequency histograms and by comparison with monthly length frequency distributions in Knight and Ross, 1992) from erosional stages II and III were used in the analyses, thus reducing potential size biases from samples containing juvenile or age-2 fish.

RESULTS

Geomorphic characterization and classification.—Determination of erosional stages (Fig. 1) showed that there is an overall trend for recent erosion (stages II–III) to be in the upper reaches of the Bayou Pierre system, with lower reaches characterized by later, recovery, stages (stages IV–V). Data from aerial imagery or field observations also show upstream movement of erosional activity. Although aerial imagery was examined for 14 sites in the Bayou Pierre watershed (S. T. Ross, D. M. Patrick, M. T. O'Connell, and C. A. Latorre, Miss. Dept. Wildl., Fish. and Parks,

1995, unpubl.; Fig. 1), we restrict our analysis to imagery sites I-3 and I-12.

Channel morphology at site I-3, located in the lower reach of Bayou Pierre near the confluence of Little Bayou Pierre, has changed very little since the 1940–1964 interval (Fig. 2). Erosion was active in 1940, as evidenced by the fresh-cut appearance of the channel bank. Imagery site I-12, located in the upper reach near Smyrna bridge, shows a canopy-covered stream channel in 1964 (and in earlier imagery), and extensive erosion was not apparent until 1978 (Fig. 2). Using the Smyrna bridge as a reference, between 1940 and 1994, the knickpoint has moved over 7 km upstream at rates of 48–750 m/yr (Table 2). Concomitantly, the channel has widened from 15–19 m before knickpoint passage, to 60–109 m following knickpoint passage (Table 3).

Temporal change in species composition.—Over all years of the study and considering all four major streams in the Bayou Pierre system, 14 species comprised 95% of the fishes collected in

TABLE 2. MOVEMENT OF THE KNICKPOINT AT SITE I-12 ON THE UPPER REACH OF BAYOU PIERRE (nd = NO DATA). Data from 1994 are based on field observations.

	Year						
	1940	1964	1978	1985	1990	1992	1994
Distance (m) between knickpoint and Smyrna bridge	-4115	-2956	-1433	122	975	1500	3000
Average knickpoint migration rate (m/yr)	nd	48	124	222	171	263	750

riffle habitats (Table 4), and five species, *Etheostoma lynceum*, *Noturus hildebrandi*, *E. rubrum*, *Cyprinella camura*, and *Etheostoma whipplei* made up almost 75% of the collections. These data are based on all population enclosures, as well as on seine hauls in riffles of stream reaches where we did not set up enclosures (generally upstream areas where *E. rubrum* did not occur).

With data adjusted for equal sampling effort over the period of study (restricted to Bayou Pierre, Foster Creek, and Turkey Creek), riffle-inhabiting fishes (Table 5) showed little temporal variation, and the four most numerous species (*E. lynceum*, *E. rubrum*, *N. hildebrandi*, and *C. camura*) were ranked in the top five every year. *Etheostoma rubrum* always was second or third in abundance in riffle habitats. The riffle assemblage, considering only a reduced set of the 15 most abundant species, was also stable over the five sample years ($W = 0.79$; $\chi^2 = 44$; $P < 0.005$). Thus, the relative abundances of *E. rubrum* and associated species have not changed significantly from 1986–1994.

Spatial and annual variation in population density.—The density of all fishes on the riffles in Bayou Pierre, Foster Creek, and Turkey Creek varied from 1–30/m² and averaged 6.7 ± 0.2 /m². Based on two-way analysis of variance ($n = 51$; restricted to Bayou Pierre and Foster Creek), total densities, and densities of *E. rubrum*, did not vary among years or between Bayou Pierre and Foster Creek, and there were not significant interactions between years and water bodies (Table 6).

To allow inclusion of additional data (i.e., from Turkey Creek and from enclosures with-

TABLE 3. CHANNEL WIDTH (m) FOR THE UPPER REACH OF BAYOU PIERRE (nd = NO DATA). Site locations are given as distance (m) below the Smyrna bridge.

Site location	Year				
	1940	1964	1978	1985	1992
-4115	19	86	87	90	109
-1400	nd	15	38	96	99
0	nd	nd	15	48	60

out *E. rubrum*), we also treated temporal and spatial aspects separately. Temporal analysis of the total density of riffle fishes, based on sample data ($n = 54$) that included Turkey Creek, also did not vary among years (Fig. 3; $F_{3,50} = 0.21$; $P > 0.05$). Considering the four numerically dominant species (Fig. 3), densities of *E. rubrum* (1.11 ± 0.17 /m²; range = 0–9/m²), *E. lynceum* (2.09 ± 0.20 /m²; range = 0–12/m²), and *N. hildebrandi* (1.12 ± 0.17 /m²; range = 0–8/m²) did not differ among years ($F_{3,50} = 0.36$; $P > 0.05$; $F_{3,50} = 2.4$; $P > 0.05$; Kruskal-Wallis $\chi^2 = 9.6$, $P = 0.022$, tablewide significance = 0.017), respectively. Densities of *C. camura* varied among years ($F_{3,50} = 5.0$; $P = 0.004$, tablewide significance = 0.013). The density was highest in 1988 at 1.46 ± 0.36 /m² and lowest in 1993–1994 at 0.36 ± 0.22 /m²; the 1988 density was significantly different from densities in 1993–1994 and 1987 (Scheffe Test, $\alpha = 0.05$).

Spatial analysis of the total density of riffle fishes, based on sample data ($n = 64$) that included Turkey Creek, showed a significant difference among streams ($F_{2,62} = 3.80$; $P < 0.05$). The density was lowest in Turkey Creek (mean = 3.28 ± 0.74 /m²) and differed significantly from the density in Foster Creek (mean = 8.42

TABLE 4. RELATIVE ABUNDANCE OF NUMERICALLY DOMINANT FISHES FROM RIFFLE HABITATS IN THE BAYOU PIERRE SYSTEM, 1986–1994.

	Number	% n	Cum. %
<i>Etheostoma lynceum</i>	2100	26.09	26.09
<i>Noturus hildebrandi</i>	1543	19.17	45.26
<i>Etheostoma rubrum</i>	1108	13.77	59.03
<i>Cyprinella camura</i>	727	9.03	68.06
<i>Etheostoma whipplei</i>	420	5.22	73.28
<i>Notropis longirostris</i>	385	4.78	78.06
<i>Cyprinella venusta</i>	383	4.76	82.82
<i>Percina vigil</i>	336	4.17	86.99
<i>Luxilus chrysocephalus</i>	146	1.81	88.81
<i>Notropis volucellus</i>	140	1.74	90.55
<i>Nocomis leptcephalus</i>	118	1.47	92.01
<i>Pimephales notatus</i>	94	1.17	93.18
<i>Pimephales vigilax</i>	70	0.87	94.05
<i>Hypentelium nigricans</i>	67	0.83	94.88

TABLE 5. NUMBERS AND ABUNDANCE RANKS (IN PARENTHESES) OF THE 15 NUMERICALLY DOMINANT SPECIES FROM BAYOU DARTER RIFFLES IN THE BAYOU PIERRE SYSTEM, 1986–1994.

	1986	1987	1988	1994
<i>Etheostoma lynceum</i>	371 (1)	706 (1)	360 (1)	378 (2)
<i>Etheostoma rubrum</i>	260 (2)	318 (2)	203 (3)	264 (3)
<i>Noturus hildebrandi</i>	165 (3)	224 (3)	91 (5)	490 (1)
<i>Cyprinella camura</i>	101 (4)	76 (4)	301 (2)	79 (5)
<i>Etheostoma whipplei</i>	61 (5)	17 (6)	6 (13)	19 (8)
<i>Luxilus chrysocephalus</i>	39 (6)	0 (14)	4 (14)	10 (9)
<i>Cyprinella venusta</i>	38 (7)	23 (5)	103 (4)	53 (6)
<i>Percina vigil</i>	22 (8)	15 (7)	71 (6)	74 (4)
<i>Ictalurus punctatus</i>	16 (9)	0 (14)	0 (15)	3 (12.5)
<i>Notropis volucellus</i>	12 (10.5)	1 (12)	12 (11)	7 (10)
<i>Noturus miurus</i>	12 (10.5)	2 (11)	9 (12)	1 (14.5)
<i>Notropis longirostris</i>	1 (15)	4 (10)	60 (7)	30 (7)
<i>Hypentelium nigricans</i>	6 (13)	8 (9)	48 (8)	3 (12.5)
<i>Pimephales vigilax</i>	6 (13)	9 (8)	41 (9)	1 (14.5)
<i>Pimephales notatus</i>	6 (13)	0 (14)	30 (10)	4 (11)

$\pm 0.30/\text{m}^2$) but not Bayou Pierre (mean = $6.05 \pm 1.75/\text{m}^2$; Scheffe Test, $\alpha = 0.05$). Because of the limited number of samples from Turkey Creek ($n = 6$), we have not presented densities of individual species.

Erosional stage and population densities.—Based on our 1993–1994 fieldwork, we analyzed variation in the total density of riffle fishes and in the density of *E. lynceum*, between erosional stages II and III, and among Bayou Pierre, Foster Creek, and Turkey Creek, using two-way ANOVA (Table 7). Variances of the other numerically dominant species were not homogeneous among erosional stages within each stream. Total density of riffle-inhabiting fishes did not vary among the main treatments but showed a highly significant interaction effect. Densities of *E. lyn-*

ceum did vary among streams and also showed a strong interaction effect. Consequently, the effects of erosion on fish density were stream dependent.

We also compared the density of all riffle-inhabiting fishes and the densities of the four most abundant species across erosional stages I–IV for Bayou Pierre only. Total density of riffle-inhabiting fishes varied across geomorphic stages, as did the densities of *E. rubrum*, *E. lynceum*, and *N. hildebrandi* (Fig. 4). In contrast, the density of *C. camura* did not vary as a function of geomorphic stage.

The spatial distribution of 1993–1994 densities of all riffle fishes (Fig. 5A) and *E. rubrum* (Fig. 5B) in the Bayou Pierre system illustrate the interactions of stream and erosional stage on densities and the generally more upstream location of *E. rubrum*. There were no *E. rubrum* taken in the population enclosures in the randomly selected riffles within geomorphic stages IV or V (although subsequent collections have shown that they do exist in the area; W. T. Slack, S. T. Ross, and J. A. Ewing III, Museum Tech. Rept. 63, Miss. Dept. Wildl., Fish. and Parks, 1998, unpubl.). Within Bayou Pierre, total densities of riffle-inhabiting fishes were higher in geomorphic stages II and III. In Foster Creek, densities of both *E. rubrum* and of all riffle-inhabiting fishes were highest in geomorphic stage III; in Turkey Creek, combined densities of all riffle-inhabiting fishes were higher in geomorphic stage III, whereas *E. rubrum* densities were greatest in stage II. In Bayou Pierre, densities of both groups were greatest in geomorphic stage II. Sites where *E. rubrum* were common were 2–3 km upstream of the Smyrna

TABLE 6. TWO-WAY ANOVA ON THE DENSITY (NUMBER/ m^2) OF ALL RIFFLE-INHABITING FISHES (A) AND BAYOU DARTERS (B) AMONG YEARS AND BETWEEN BAYOU PIERRE AND FOSTER CREEK.

Source	df	mean square	F	P
(A)				
stream	1	0.96	2.14	0.15
year	3	0.08	0.18	0.91
stream \times year	3	0.24	0.52	0.67
residual	43	0.45		
(B)				
stream	1	0.22	0.67	0.42
year	3	0.13	0.38	0.76
stream \times year	3	0.19	0.56	0.65
residual	43	0.33		

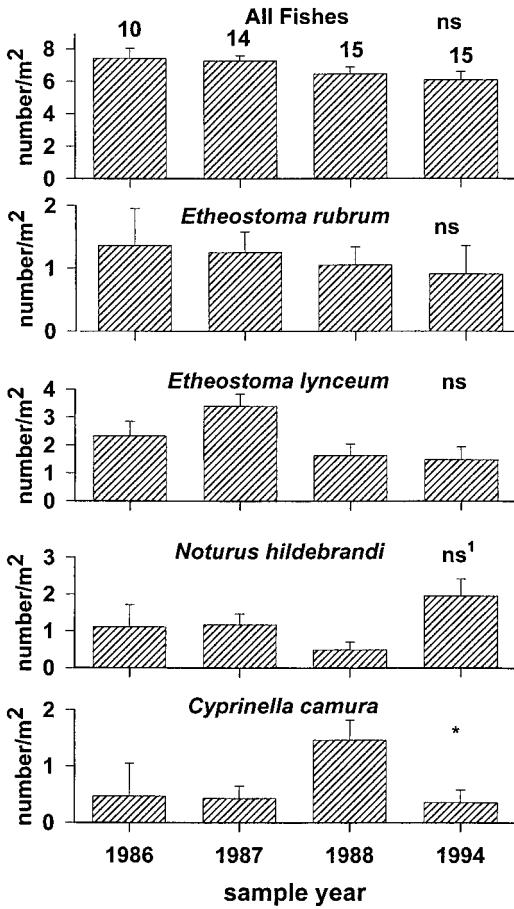


FIG. 3. Densities of all riffle-inhabiting fishes in enclosure samples (from bayou darter localities) in the Bayou Pierre system. Vertical lines are 95% CI.

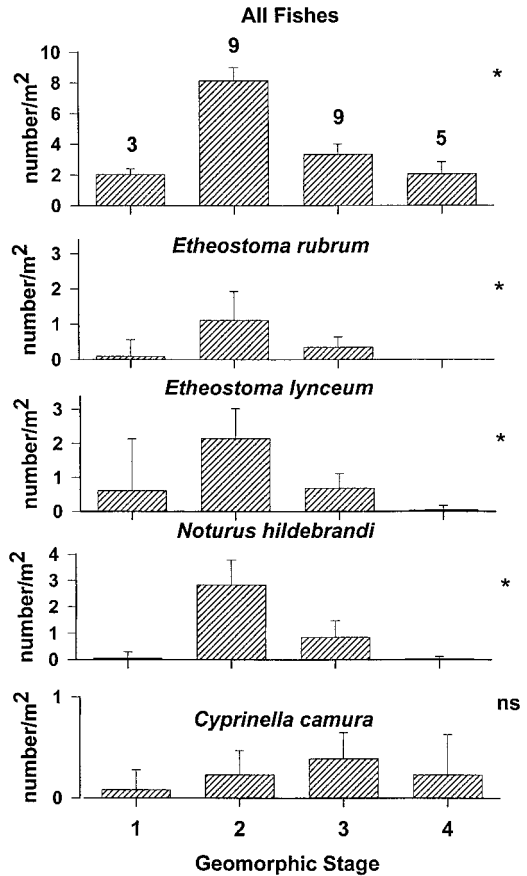


FIG. 4. Densities of all riffle-inhabiting fishes and the four numerically dominant species in 1993–1994 enclosure samples from Bayou Pierre. Vertical lines are 95% CI; asterisks indicate significant differences. Differences for total riffle fishes tested with ANOVA ($F = 4.04$; $P = 0.012$); differences for individual species tested with K-W with α corrected for multiple comparisons (*Etheostoma rubrum*, $\chi^2 = 12.5$, $P = 0.006$; *Etheostoma lynceum*, $\chi^2 = 11.4$, $P = 0.010$; *Etheostoma hildebrandi*, $\chi^2 = 12.0$, $P = 0.007$; *Cyprinella camura*, $\chi^2 = 1.9$, $P = 0.592$).

TABLE 7. TWO-WAY ANOVA ON THE DENSITY OF ALL RIFFLE-INHABITING FISHES (A) AND *Etheostoma lynceum* (B) BETWEEN GEOMORPHIC STAGES II AND III AND AMONG BAYOU PIERRE AND FOSTER AND TURKEY CREEKS.

Source	df	mean square	F	P
(A) Total density				
stream	2	0.71	1.98	0.15
geo. stage	1	0.10	0.29	0.59
stream × geo. stage	2	3.54	9.84	0.000
residual	41	0.36		
(B) <i>Etheostoma lynceum</i>				
stream	2	0.96	3.14	0.05
geo. stage	1	0.35	0.11	0.74
stream × geo. stage	2	1.84	6.00	0.005
residual	41	0.31		

bridge. Just above the headcut in Bayou Pierre (i.e., geomorphic stage I), densities of all riffle-inhabiting fishes (and thus also *E. rubrum*) were again $< 1/m^2$.

Erosional stage and Etheostoma rubrum condition.—We tested for differences in mass-length relationships between erosional stages II and III, using only age-1 *E. rubrum*. During 1993–1994, 12 males and 51 females were collected from riffles in erosional stage II. Males averaged 29.7 mm SL ($s = 1.96$, range 27.5–32.5) and 0.44 g ($s = 0.09$, range 0.33–0.61 g); females averaged 29.1 mm SL ($s = 1.29$, range 27.0–32.0) and 0.40 g

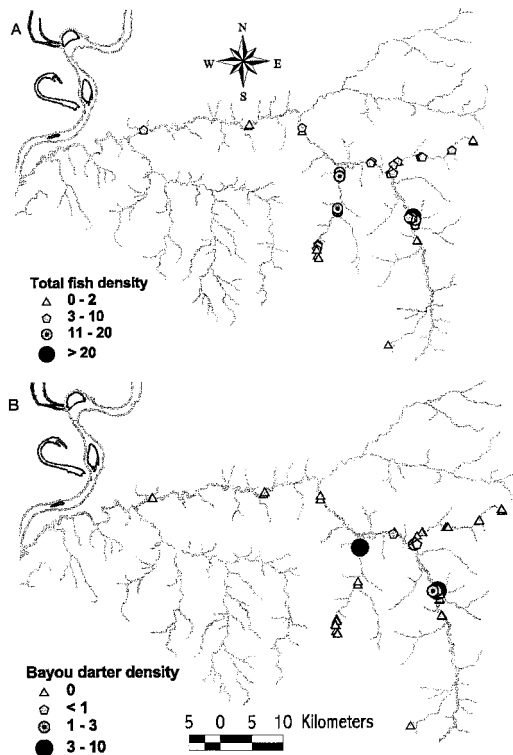


FIG 5. Spatial distribution of the density (number/m²) of all riffle fishes (A) and *Etheostoma rubrum* (B) in the Bayou Pierre system, Mississippi.

($s = 0.05$, range 0.30–0.49 g). Twenty males and 66 females were collected from riffles in erosional stage III. Males averaged 30.5 mm SL ($s = 1.29$, range 27.0–32.6) and 0.49 g ($s = 0.11$, range 0.25–0.65 g); females averaged 29.5 mm SL ($s = 1.75$, range 27.0–32.6) and 0.46 g ($s = 0.12$, range 0.23–0.67 g). Condition, as evidenced by the adjusted means and slopes of length-weight relationships of all age-1 *E. rubrum* (Fig. 6), did not differ between riffles in erosional stages II and III ($F_{1,150} = 0.013$, $P = 0.91$, slopes equal: $P = 0.75$). When the data were split by sex, the same pattern of no change between erosional stages held (males: $F_{1,28} = 0.639$, $P = 0.43$, slopes equal: $P = 0.05$; females ($F_{1,117} = 0.317$, $P = 0.57$, slopes equal: $P = 0.31$).

DISCUSSION

Geomorphic characterization and classification.—Aerial imagery and observations on the ground indicate that erosion is active within the Bayou Pierre system. Generally, the style of erosion is knickpoint migration or headcutting (Patrick et al., 1991). Headcutting is particularly active upstream of the Smyrna bridge along the main

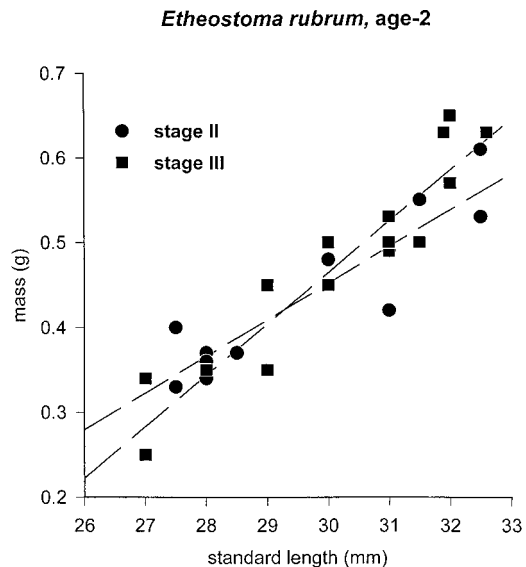


FIG 6. Condition of *Etheostoma rubrum*, as indicated by mass-length relationships, from geomorphic stages II and III in Bayou Pierre, 1993–1994.

channel of Bayou Pierre; however, it is also occurring along upstream tributaries such as Foster Creek.

Although land cover and land use changes have occurred and are occurring in the watershed, there is no particular evidence that these changes have contributed significantly to the on-going channel erosion. For example, studies in north Mississippi, which has experienced significant and widespread historical changes in land use and land cover, show that these changes result in increased sedimentation, channel in-filling, and flooding in the upstream reaches (S. C. Happ, G. Rittenhouse, and G. C. Dobson, U.S. Dept. Agriculture Tech. Bull. 695, Washington, DC, 1940, unpubl.). In these upstream reaches, channel and bank erosion was not a problem until channelization and related activities were conducted along and at downstream reaches (C. B. Whitten and D. M. Patrick, Tech. Rept. GL-79-7, U.S. Army Engineer Waterways Experim. Sta., 1981, unpubl.; Schumm et al., 1984). Also, we see no particular differences between the style of headcutting observed in Bayou Pierre and that seen in north Mississippi. Therefore, our evidence indicates that the causes of the headcutting have originated downstream in lower parts of the system.

Causes of headcutting are difficult to discern but may include the following: (1) natural meander cut-offs on either Bayou Pierre or the Mississippi River; (2) Mississippi River avulsion (an avulsion is the abandonment of a course

and the occupying of a new or former course); (3) channelization (i.e., the straightening of the channel of either Bayou Pierre or the Mississippi River for navigation or flood protection purposes); (4) in-channel mining of sand and gravel bars in Bayou Pierre (S. T. Ross, D. M. Patrick, M. T. O'Connell, and C. A. Latorre, Miss. Dept. Wildl., Fish. and Parks, 1995, unpubl.; M. D. Patrick, unpubl.). Perhaps the greatest contributors to headcutting have been natural and human-made cut-offs on the Mississippi River resulting in shortening of the channel and thus increases in stream gradient (Albertson and Patrick, 1996). One natural cut-off occurred in 1776 in the Mississippi River near the mouth of the Homochitto River (downstream of the confluence of Bayou Pierre; Albertson and Patrick, 1996). Since 1931, there have been five artificial cut-offs in the Mississippi River downstream of Bayou Pierre. Overall, these changes have shortened the Mississippi River in this region by 121 km (B. R. Winkley, U.S. Army Engineer District, Vicksburg, Potamology Invest. Rept., 1977, unpubl.; Albertson and Patrick, 1996). Channelization has been less of a factor in Bayou Pierre than in the Mississippi River, although Little Bayou Pierre has been shortened by about 250 m because of channelization taking place between 1940 and 1964 (D. M. Patrick, L. Mao, and S. T. Ross, Museum Tech. Rept. 18, Miss. Dept. Wildl., Fish. and Parks, 1991, unpubl.).

Temporal and spatial changes in species composition.—Even though the Bayou Pierre System has been undergoing extensive erosion, and the physical position of riffles has frequently changed (Patrick et al., 1991; pers. obs., 1986–1994), the riffle-inhabiting fish assemblage has maintained its integrity. Densities of all riffle-inhabiting fishes, as well as densities of three of the four most abundant species (*E. rubrum*, *E. lynceum*, *N. hildebrandi*), have also remained stable over time; only the density of *C. camura* varied temporally. Spatial variation in density of all riffle-inhabiting fishes between Bayou Pierre and Foster Creek was also insignificant, but densities were lower in Turkey Creek. Other long-term studies have shown strong effects of environmental variation (flow regime) on assemblage structure (Grossman et al., 1998). However, our focus on riffle assemblages has likely eliminated such variation, which was primarily a result of changes in water-column depth.

The impact of headcutting on the population density of riffle-inhabiting fishes is generally stream dependent. Within Bayou Pierre, densities of all riffle-inhabiting fishes and of all common species except *C. camura* varied among

erosional stages I–IV, with highest densities in stages II and III. The trend for the greatest density of *E. rubrum* in the zone of active headcutting supports earlier suggestions (Ross et al., 1992) that *E. rubrum* have moved upstream following the zone of active erosion. *Etheostoma rubrum* are now common at least 2–3 km upstream of the Smyrna bridge, and Ross et al. (1992) reported a single individual over 23 km (straight-line distance) upstream of Smyrna. However, in surveys of Bayou Pierre from 1963 into the 1970s by Suttkus and Clemmer (1977), and in 1974–1975 by Teels (1976), the most upstream collection of *E. rubrum* was 7.5 km (channel distance) downstream from the Smyrna bridge. Matthews (1978), based on fieldwork done in 1977 and 1978, categorized *E. rubrum* as present but uncommon in the Smyrna bridge area of Bayou Pierre. The only area where *E. rubrum* were considered abundant was at the confluence of Bayou Pierre with White Oak Creek.

Mass-length data indicate that *E. rubrum* occupying newly eroding areas do not suffer reduced body condition. Although no *E. rubrum* were taken in population enclosures in geomorphic stage IV, our earlier studies indicate that *E. rubrum* have been present in the lower reaches of Bayou Pierre (Ross et al., 1990, 1992) and subsequent fieldwork (W. T. Slack, S. T. Ross, and J. A. Ewing III, Museum Tech. Rept. 63, Miss. Dept. Wildl., Fish. and Parks, 1998, unpubl.) has further verified this.

Populations in both Turkey and Foster Creeks are also moving upstream following the headcut. In this study, we have documented the furthest upstream collection of *E. rubrum* in Foster Creek. However, in both creeks, *E. rubrum* have their highest densities in geomorphic stage III. As a consequence, these populations have survived passage of the headcut.

Although we have demonstrated that *E. rubrum* and associated riffle-inhabiting fishes have generally maintained population densities in spite of substantial habitat change, other faunal components of the Bayou Pierre system have been negatively impacted. For instance, populations of unionid mussels are negatively impacted by sediment deposition and bed mobility (Vaughn and Taylor, 1999) and have shown drastic declines following passage of the headcut in Bayou Pierre (Hartfield and Ebert, 1986). In addition, increased sedimentation has apparently resulted in loss of deeper pools, based on comments from local landowners (STR, pers. obs., 1986–1994). Such changes have likely had a negative effect on larger fish species (e.g., *Ictalurus* spp., *Ictiobus* spp., *Carpiodes* spp.), which

tend to occupy deeper habitats (Harvey and Stewart, 1991; Matthews, 1998; Ross, 2001). However, there are no data on long-term population trends of these larger species in Bayou Pierre.

Conclusions.—Ongoing geomorphic changes in the Bayou Pierre system have resulted in upstream shifts in riffle-inhabiting fishes but have generally not affected population densities of numerically dominant species. Ultimate factors responsible for the rapid headcutting are located downstream of currently affected reaches, perhaps originating within the Mississippi River. Thus, river-management decisions impacting areas spatially distant from the study area appear to have resulted in major local changes. These results support other studies of stream fish assemblages (e.g., Schlosser 1991; Grossman et al., 1995) in emphasizing the importance of a landscape approach to habitat management.

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