

## Ecology and population structure of the bayou darter, *Etheostoma rubrum*: disjunct riffle habitats and downstream transport of larvae

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### Synopsis

The bayou darter, *Etheostoma rubrum* (Percidae), is endemic to the Bayou Pierre system in Mississippi. Adult and juvenile *E. rubrum* occupy swift, shallow riffles or runs over coarse gravel and pebble substrata. Habitat requirements of larval and post-larval stages, and the role of downstream dispersal of larvae in colonizing riffles are poorly known. The potential for movement and the high level of habitat specificity for the discontinuous riffle habitat suggest that *E. rubrum* may comprise a metapopulation of linearly arranged local populations. The greatest population densities of *E. rubrum* occur in the upper reaches of Bayou Pierre. We hypothesized that metapopulation structure of *E. rubrum* may include source–sink dynamics, whereby downstream areas are a sink for larvae/early juveniles originating upstream. We tested hypotheses that a transport mechanism, larval drift, occurred in *E. rubrum*, and that downstream riffles showed characteristics of population sinks. We captured larval stages of *E. rubrum* in cross-sectional and longitudinal drift nets, and rates of drift tended to increase during the day. Larval *E. rubrum* (n = 19) occurred in samples above and below riffle areas, with no differences among longitudinal drift nets placed above and below riffles. Thus, larval drift is a viable transport mechanism. Relative abundance of adults and juveniles declined from upstream to downstream, and inter-riffle distances increased with cumulative downstream distance. However, both predictions of the source–sink hypothesis were not supported. The distribution of size classes did not change between upstream and downstream riffles nor did the mean size-adjusted body mass.

### Introduction

*Etheostoma rubrum* (bayou darter, Percidae, subgenus *Nothonotus*) is endemic to the Bayou Pierre system in western Mississippi (Teels 1976, Suttkus & Clemmer 1977, Ross et al. 1992). Because of its limited natural range, and especially because of ongoing habitat degradation in Bayou Pierre and its tributaries, it is listed as ‘threatened’ under the Endangered Species Act (USFWS<sup>1</sup>) and as ‘endangered’ by the

state of Mississippi (Mississippi Museum of Natural Science<sup>2</sup>).

<sup>1</sup> United States Fish and Wildlife Service 1999. U.S. listed vertebrate animal species index by lead region and status as of 31 December 1999. From USFWS Service ‘Endangered Species Home Page’ available from the Internet URL <http://endangered.fws.gov/wildlife.html#Species>

<sup>2</sup> Mississippi Museum of Natural Science 2001. Endangered species of Mississippi. Mississippi Department of Wildlife, Fisheries and Parks, Museum of Natural Science, Jackson, Mississippi. 123 pp.

*Etheostoma rubrum* is a habitat specialist, with late-stage juveniles and adults occupying swift, shallow riffles or runs over coarse gravel and pebble substrata. Current speeds in such riffles average  $.79 \text{ m s}^{-1}$ , and fish are usually found over substrata 16–64 mm in diameter; they are only rarely collected over small gravel (Ross et al. 1992). Based on a laboratory stream system, spawning sites chosen by *E. rubrum* are in very coarse sand (1–2 mm), in contrast to the coarse gravel and pebbles selected by non-spawning individuals (Ross et al. 1992). The fertilized eggs are buried in clumps in the sand and hatching occurs in 7 days at a water temperature of 21–23°C (Ross & Wilkins 1993).

Little is known about habitat requirements of larval and post-larval stages of *E. rubrum* and the role of downstream dispersal of larvae in colonizing riffle habitats. As recognized by many fish ecologists, events occurring during the egg to post-larval stages may largely control subsequent population success (e.g., Schlosser 1985). Movement patterns have not been studied for *E. rubrum* and available information seems equivocal. Longitudinal dispersal of individual *E. rubrum* within a stream, or movement among streams in the Bayou Pierre system, may be limited because of extreme habitat specificity. For instance, within the Bayou Pierre system *E. rubrum* is absent from some streams with apparent suitable habitat (e.g., Little Bayou Pierre and Tallahalla Creek) (Ross et al. 1990). However, evidence in support of movement is two-fold. First, based on previous efforts (Ross et al. 1992), most individuals captured at downstream sites in Bayou Pierre are juveniles or females. Although they do occur downstream, male *E. rubrum* are less numerous in these areas, compared to more upstream sites, suggesting either juvenile mortality or an upstream movement pattern of maturing fish (Ross et al. 1992). Second, based on allozyme data, there are apparently no genetic differences between *E. rubrum* in the two main branches of the Bayou Pierre system occupied by *E. rubrum* (Bayou Pierre and Foster Creek) (R. Wood, St. Louis University 1994, personal communication, Wood 1996).

The potential for larval or early juvenile movement, coupled with the high level of habitat specificity for discontinuous, coarse-bottomed riffle habitat suggests that *E. rubrum* may be viewed as a

metapopulation (Hanski & Simberloff 1997, Gotelli & Taylor 1999) comprising linearly arranged, local populations. In recent population studies of *E. rubrum*, based on a random, stratified sampling program, we have shown that the greatest population densities were in the upper reaches of Bayou Pierre in areas of active erosion (stage II, cf. Schumm et al. 1984), or just below such areas (stage III, Ross et al. 2001). Consequently, we hypothesize that metapopulation structure of *E. rubrum* may include source–sink dynamics (sensu Pulliam 1988), whereby downstream local populations are a sink for larvae or early juveniles originating from high population densities in upstream riffle areas. If local populations in lower reaches are sinks, then the source–sink hypothesis would predict that age structure should differ between the more abundant upstream local populations and the smaller downstream local populations. In addition, size-adjusted masses of *E. rubrum*, a measure of condition, should be less in downstream than in upstream riffles, if downstream riffles represent a poorer quality habitat.

Our objectives were to test hypotheses that: (1) a transport mechanism, larval drift, occurs in *E. rubrum*, and (2) downstream riffles show characteristics of sinks. Specifically, we determined the diel timing of greatest larval drift, the degree of downstream transport of larval and early juvenile *E. rubrum*, the relative abundance and population size structure of *E. rubrum* in the mid and lower reaches of Bayou Pierre, and potential differences in age structure and condition between upstream and downstream populations of *E. rubrum*.

## Materials and methods

### *Sampling of larvae*

All sampling occurred in Foster Creek (Copiah County), a third order tributary of Bayou Pierre (Figure 1). Sampling was restricted to the lower 3 km of the stream (T01N, R04W, Sec 8, 9, 16, 17) which is characterized as erosional stage III (hereafter termed stage) and which supports high densities of *E. rubrum* (Ross et al. 2001). Larval sampling occurred during summer low-flow within the known (April through August) spawning period of *E. rubrum* (Knight & Ross 1992).

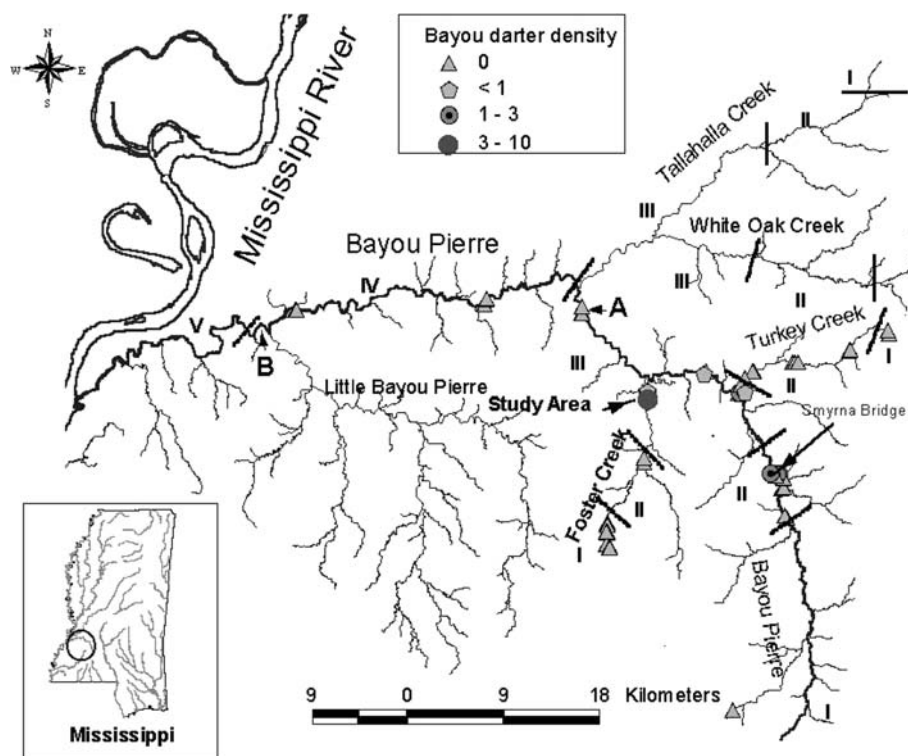


Figure 1. The Bayou Pierre system with locations of major streams and erosional stages (indicated by Roman numerals, following Schumm et al. 1984). Densities of *Etheostoma rubrum* are given as number per m<sup>2</sup> (Ross et al. 2001). Study area (solid circle) indicates the site for larval studies on Foster Creek; A and B show the beginning and end of the sampled reach for juvenile and adult *E. rubrum*.

To determine the degree of downstream transport of larval and early juvenile stages of *E. rubrum*, we used a longitudinal configuration of five drift nets (600  $\mu$ m mesh, Nitex drift nets, 31 cm  $\times$  31 cm  $\times$  1.3 m with removable PVC collecting container, Aquatic Research Instruments) set above and below riffles. For each longitudinal array, we positioned the first and second drift nets upstream of the selected riffle, the third drift net immediately downstream of the selected riffle, and nets four and five further downstream of the riffle. Because all sampled riffles were not the same length, exact spacing of the drift nets varied relative to the total length of the sampled stream reach with nets positioned approximately equidistant along the transect above and below the riffle. Total transect lengths were 26–53 m ( $\bar{x}$  = 38 m) with the riffle positioned approximately in the middle of the transect. The placement of nets above potential riffle spawning areas was necessary to determine if larvae were being transported downstream from

more upstream spawning sites. There was not another riffle within several hundred meters upstream of each study riffle. In addition, we used a configuration of three drift nets placed across the downstream region of a shallow riffle (i.e., cross-sectional samples) to supplement the data from the longitudinal sets for determining diel periodicity of larval drift.

We secured all nets by driving short pieces of metal conduit through the net frame and into the stream bottom. We chose riffles that had areas of coarse sand (the site of egg deposition for *E. rubrum*, Ross & Wilkins 1993), and prior to all drift sets, we sampled riffles with 3–5 kick sets (cf., Hendricks et al. 1980) using a 1.2  $\times$  3.1 m seine with 3.2 mm Ace mesh to verify the presence of reproductively mature *E. rubrum*. We conducted three longitudinal riffle samples from 2 June to 7 July 1997 and four cross-sectional riffle samples from 22 May to 7 July 1997. We sampled both configurations at approximately 2 week intervals.

Nets were fished for 20 min periods at 4 h intervals over 24 h. Larval fishes were fixed in the field and maintained in 3–5% buffered formalin.

Larval characteristics of *E. rubrum* were described by Ross & Wilkins (1993), using Snyder's (1976) terminology for characterization of larval stages, and we have retained that terminology in this paper. Based on an alternative terminology of the life history model (Balon 1990, 1999), *E. rubrum* and other percids in our study would have an indirect life history, characterized by free embryo, finfold larval, and fin-formed larval phases.

We identified larvae to the lowest possible taxon aided by reference collections, descriptions in Ross & Wilkins (1993), and by working back through representative series (i.e., juvenile, metalarvae, mesolarvae, protolarvae). All specimens are catalogued into the University of Southern Mississippi (USM) Museum of Ichthyology.

#### *Adult and juvenile sampling*

To assess the relative abundance and population size structure of adult *E. rubrum* in the lower reaches of Bayou Pierre, we sampled approximately 40 km of Bayou Pierre, from several km upstream of the confluence with White Oak Creek (Mississippi Highway 18 bridge crossing) downstream to the confluence of Little Bayou Pierre (Claiborne Co.) (Figure 1). Bayou Pierre in the vicinity of Mississippi Highway 18 is characterized as a fourth order stream and stage III, whereas the remaining lower reach is characterized as fifth order and stage IV (Ross et al. 2001). Sampling of the area occurred during low-flow on 12–13 and 26–28 September 1997 and on 26–28 October and 3 November 2001. To access riffles, we floated the river by canoe and recorded the location (Universal Transverse Mercator coordinates, map projection NAD 1927) for each visible riffle with GPS units (1997 – Magellan 2000; 2001 – Garmin GPS 12XL). Using a 1.2 × 3.1 m seine (3.2 mm Ace mesh) and five kick sets, we sampled the first riffle encountered on each section floated (i.e., each day), then sampled riffles 5, 10, 15, etc. In floated stream sections where riffles were less common, we sampled every third riffle. All captured *E. rubrum* were lightly anesthetized with tricaine methane sulfonate (MS-222) prior to measuring, following the techniques of Stickney (1983). We measured fish to the nearest

0.5 mm standard length (SL) using a 150 mm plastic ruler and weighed them to 0.01 g (wet mass) using a portable electronic field balance (Ohaus®, model CT 200-S; ACCULAB®, model V-200). We categorized individuals as male, female or juvenile based on coloration and size (Raney & Suttkus 1966, Knight & Ross 1992). Following measurements, we placed the fish in a bucket of stream water until they had resumed normal activity, after which we released them at the point of original collection. We identified all remaining fishes and enumerated them in the field after completing the five kick sets, and then released them into the stream in the vicinity of original collection.

#### *Statistical analyses, larval sampling*

We standardized raw abundance values for drift samples to adjust for the difference in current velocity among all nets and abundance is reported as individuals per 100 m<sup>3</sup> of filtered water. We calculated the amount of filtered water by multiplying mean velocity (m s<sup>-1</sup>) by mean depth (cm), net width, and soak time. We computed mean velocity and depth from point samples taken at 0.5 m intervals along a transect extending 5 m upstream of each net. We used the height of the drift net (31 cm) when mean depth exceeded net height.

We determined drift periodicity by combining standardized abundance data for both cross-sectional and longitudinal drift samples. We used a Kruskal–Wallis test to assess whether a significant pattern of periodicity was apparent. We corrected ranked values for ties (Siegel 1956). We assessed patterns in downstream transport (longitudinal drift) with a Kruskal–Wallis test with ranked values corrected for ties (Siegel 1956). We tested statistical significance with  $\alpha = 0.05$  for all analyses. We used a sequential Bonferroni method to yield a table-wide significance level (Holm 1979, Rice 1989) when multiple, independent comparisons were made from a single dataset.

#### *Statistical analyses, adults and juveniles*

We determined age structure of *E. rubrum* from length-frequency histograms and by comparison with length-frequency distributions in Knight & Ross (1992). We compared frequency distributions of size classes using a Kolmogorov–Smirnov two

sample test to assess differences in age structure between upstream and downstream samples (essentially between stages III and IV), and between survey periods (1997, 2001). We compared mass-length relationships (growth) between males and females obtained from both survey periods (1997, 2001) using analysis of covariance (ANCOVA). We also used ANCOVA to determine slopes (a measure of growth) and size-adjusted mean mass (condition) between downstream (stage IV) and upstream reaches (stages II and III). We included data from 1993 to 1994 based on Ross et al. (2001) as well as data from 1997 and 2001. We rank-transformed data (RT-2) (Conover & Iman 1981) prior to analyses. We used a conservative alpha level (0.01) to protect against an increase in Type I error (Winer et al. 1991) because of marginal heteroscedasticity and the disparity in sample sizes among comparative groups (i.e., year, sex, erosional stage). All data were analyzed with SIMSTAT v1.21d (Péladeau 1996).

We determined the distance between each riffle in the lower section of Bayou Pierre by using the measure function in Atlas GIS 3.0 and ArcView GIS 3.2. We then calculated both simple and moving averages (group size = 3) of inter-riffle distances vs. cumulative river distance, going in an upstream to downstream direction.

## Results

### Larval sampling

Based on all drift sets (longitudinal and cross-sectional), larval percids (including proto- and mesolarval stages of *Ammocrypta* spp. (n = 6), *Etheostoma lynceum* (n = 2), *E. rubrum* (n = 27) and *Etheostoma* spp. (n = 37)) did not differ in drift abundance among the six time periods (Kruskal-Wallis  $\chi^2 = 7.60$ ,  $p = 0.180$ ). Separate analyses of *E. rubrum* (Kruskal-Wallis  $\chi^2 = 8.48$ ,  $p = 0.132$ ) and the remaining congeneric larvae (*Etheostoma* spp.; Kruskal-Wallis  $\chi^2 = 3.57$ ,  $p = 0.467$ ) yielded the same result. As was true for all larval percids, larval *E. rubrum* tended to be more abundant during the day (Figure 2), and when samples were grouped by day (1000–1800 h) and night (2200–0600 h), the difference in abundance approached significance (Kruskal-Wallis

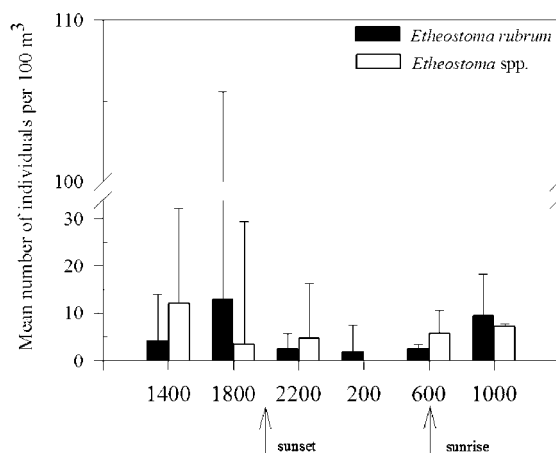


Figure 2. Diel drift periodicity of larval *Etheostoma* in Foster Creek, Copiah County, Mississippi. The *Etheostoma* spp. grouping includes *Etheostoma lynceum* and additional taxa that were not identifiable to species.

$\chi^2 = 4.85$ ,  $p = 0.028$ ; table-wide significance level  $p = 0.025$ ); *Etheostoma* spp. did not differ in drift abundance between grouped day and night samples (Kruskal-Wallis  $\chi^2 = 0.003$ ,  $p = 0.961$ ).

Ranked abundances for all larval percids did not differ among the five longitudinally placed nets (Kruskal-Wallis  $\chi^2 = 6.41$ ,  $p = 0.170$ ). Larval *E. rubrum* occurred in samples above and below riffle areas, and there was not a significant difference among nets in ranked standardized abundance (Kruskal-Wallis  $\chi^2 = 6.11$ ,  $p = 0.191$ ) (Figure 3). In contrast, congeneric percid larvae (*Etheostoma* spp.) only occurred downstream of riffles (nets 3–5) but showed no significant difference in abundance among downstream nets (Kruskal-Wallis  $\chi^2 = 2.00$ ,  $p = 0.368$ ). However, these results should be considered with some degree of caution. Mean upstream water velocity differed significantly among nets ( $F_{(4,228)} = 22.27$ ,  $p = 0.001$ ) with nets 1 and 2 being in slower currents than nets 3 and 4 (Figure 3). Although abundance values were standardized for differences in velocity among nets, standardized values for low velocities may have overestimated numbers of larvae. Of the 14 samples that contained larval *E. rubrum* or *Etheostoma* spp., one contained three individuals, three contained two individuals and the remaining 10 were represented by a single individual. Examining the frequency of occurrence of *E. rubrum* among all nets, regardless of velocity

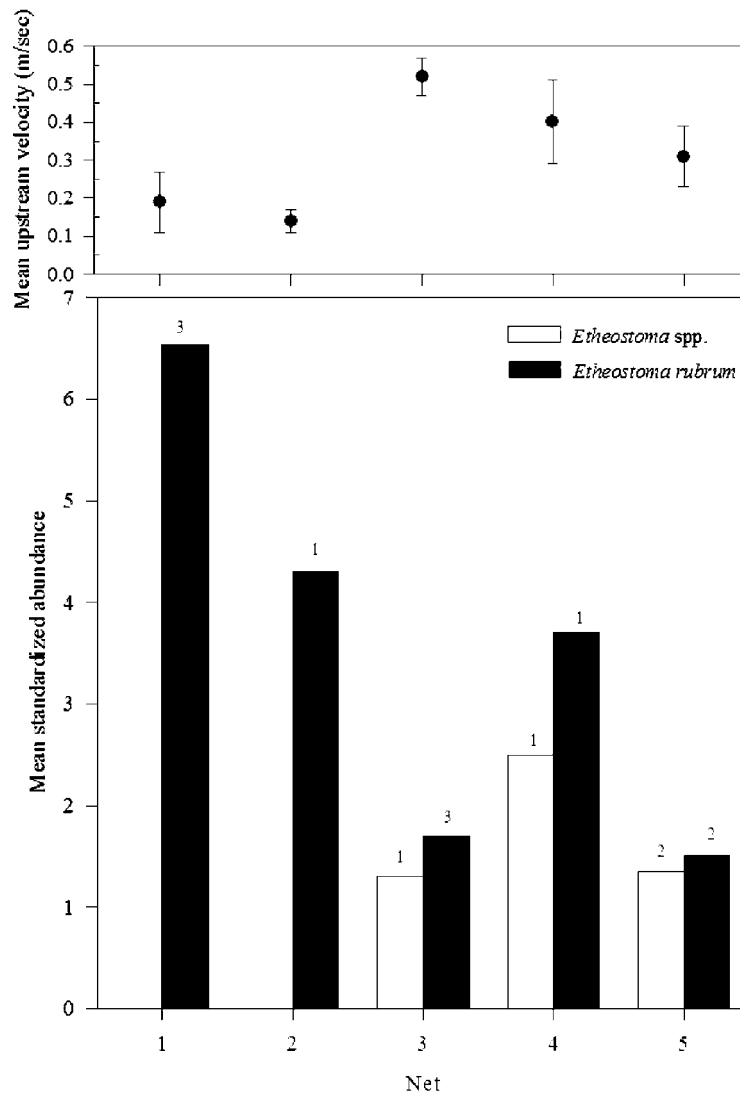


Figure 3. Upper panel: Mean upstream velocity for the longitudinal array of drift nets; nets 1–2 were above a riffle; nets 3–5 were below a riffle. Vertical bars indicate 95% confidence intervals. Lower panel: Standardized abundances of *Etheostoma rubrum* and *Etheostoma* spp. larvae in drift nets above and below riffles. Numbers above bars note the frequency of specific drift samples containing *Etheostoma rubrum* or *Etheostoma* spp.

or abundance (raw or standardized), however, indicates no significant difference in the frequency of occurrence when the probability of occurrence was considered equal among all nets ( $\chi^2_{df=4} = 2.00$ ,  $p = 0.864$ ).

#### Riffle habitats and adult–juvenile sampling

In 1997, we documented 88 riffles along the lower reach of Bayou Pierre from Mississippi Highway

18 to the confluence with Little Bayou Pierre, 24 of which we sampled for *E. rubrum* (Figure 4). *Etheostoma rubrum* occurred in 19 riffles (79.2%) with 1–14 ( $\bar{x} = 6$ ) individuals present in the sampled areas. We collected a total of 104 *E. rubrum* from the entire lower reach, consisting of 47 juveniles, 22 males, and 35 females. The percent occurrence of *E. rubrum* in the sampled riffles was greater within stage III than IV (Table 1). We documented 12 riffles in stage III, we sampled

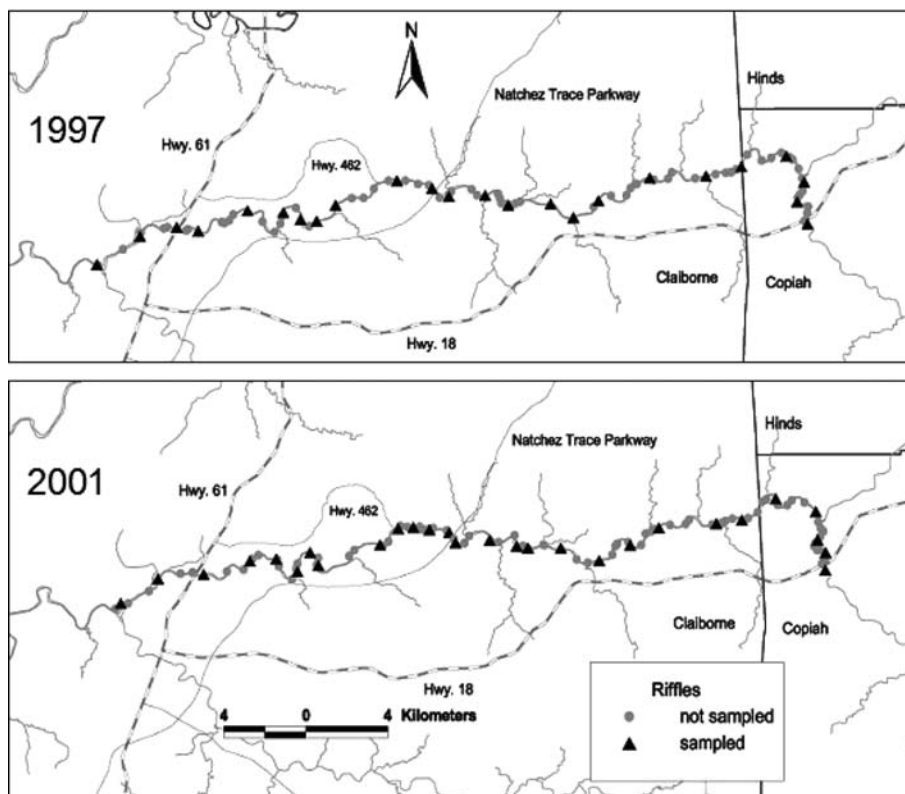


Figure 4. The lower section of Bayou Pierre (MS Highway 18 to the confluence with Little Bayou Pierre) showing the location of all riffles and riffles sampled for *Etheostoma rubrum* during 1997 (upper panel) and 2001 (lower panel).

Table 1. Number of *Etheostoma rubrum* processed during 1997 and 2001 surveys of lower Bayou Pierre from MS Highway 18 to the confluence with Little Bayou Pierre.

Year	Erosional stage	Riffles sampled	Juvenile	Male	Female	Total processed
1997	III	4	9 (100)	13 (100)	9 (100)	31 (100)
1997	IV	20	38 (60)	9 (40)	26 (35)	73 (70)
Total		24	47	22	35	104
2001	III	4	5 (50)	22 (75)	99 (100)	126 (100)
2001	IV	24	18 (38)	22 (46)	144 (83)	184 (83)
Total		28	23	44	243	310

Numbers in parentheses are percent occurrences of *E. rubrum* by category within sampled riffles.

four, and all contained *E. rubrum*. The remaining 76 riffles were in stage IV; we sampled 20, and 14 (70%) had *E. rubrum* present. In 2001, we documented 100 riffles along the same lower reach of Bayou Pierre and sampled 28 (Figure 4). We collected *Etheostoma rubrum* in 24 riffles (85.7%) with 1–91 ( $\bar{x} = 11$ ) individuals per sampled riffle.

Overall, we collected 310 *E. rubrum* comprising 23 juveniles, 44 males, and 243 females (Table 1).

In both 1997 and 2001, longitudinal patterns of relative abundance showed a gradual decline from upstream to downstream riffles (Figure 5). In part, this pattern seems to be driven by habitat quality with more upstream riffles tending to have firm,

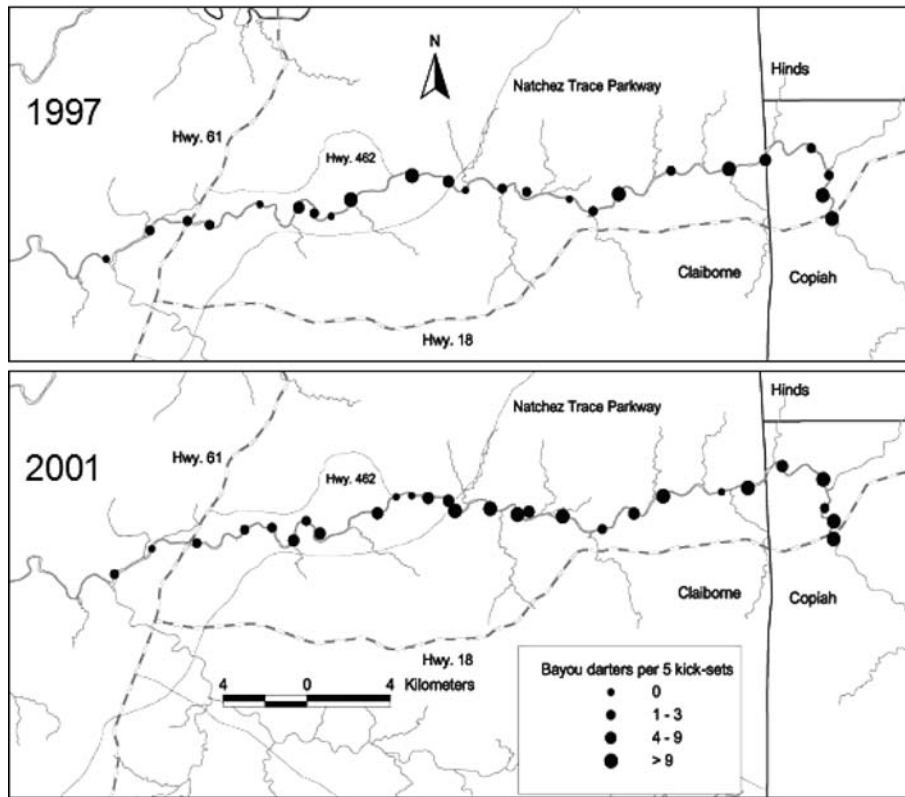


Figure 5. The lower section of Bayou Pierre (Mississippi Highway 18 to the confluence with Little Bayou Pierre) showing relative abundances of *Etheostoma rubrum* during the 1997 (upper panel) and 2001 (lower panel) survey periods. Numbers are based on five standardized kick-sets at each locality.

coarse substrata and downstream riffles generally having gravel and pebbles forming a veneer over fine materials. Details of habitat characteristics are given in Ross et al.<sup>3</sup> and Slack & Ross.<sup>4</sup>

The apparent downstream decline in the number of riffles per km (Figure 4) is supported by significant correlations (1997:  $r = 0.37$ ,  $p < 0.001$ ; 2001:  $r = 0.53$ ,  $p < 0.001$ ) between the moving average of inter-riffle distance vs. cumulative downstream distance (Figure 6). Most of the increase in inter-riffle distance occurs at the transi-

tion between stages III and IV (cf., Figures 1 and 4). When only inter-riffle distances in stage IV are examined, the correlation decreases but remains significant (1997:  $r = 0.24$ ,  $p < 0.02$ ; 2001:  $r = 0.40$ ,  $p < 0.001$ ).

#### Age structure and condition

Size and inferred age structure of *E. rubrum* did not differ between the 1997 and 2001 surveys (K-S  $Z_{(16)} = 0.884$ ,  $p = 0.415$ ). We categorized fish  $\leq 24$  mm SL as Age 0, 25–34 mm as Age I, 35–44 mm as Age II, and  $>44$  mm SL as Age III (Figure 7), following Knight & Ross (1992). The source-sink prediction of altered age structure in downstream riffles was not supported as there was no difference in size structure between upstream (stage III) and downstream (stage IV) riffles in 1997 (K-S  $Z_{(16)} = 0.530$ ,  $p = 0.941$ ) or in 2001 (K-S  $Z_{(16)} = 0.177$ ,  $p = 1.000$ ). However, fish

<sup>3</sup>Ross, S.T., D.M. Patrick, M.T. O'Connell & C. Latorre. 1995. Population dynamics of the bayou darter – the impact of geomorphic change, Final Report, U.S. Fish & Wild. Serv. and Mississippi Department of Wildlife, Fisheries and Parks, Project E1-Segment 9, Jackson. 70 pp.

<sup>4</sup>Slack, W.T. & S.T. Ross. 2001. A survey of lower Bayou Pierre for bayou darters (*Etheostoma rubrum*), Museum Technical Report No. 96. Mississippi Department of Wildlife, Fisheries and Parks, Museum of Natural Science, Jackson. 20 pp.

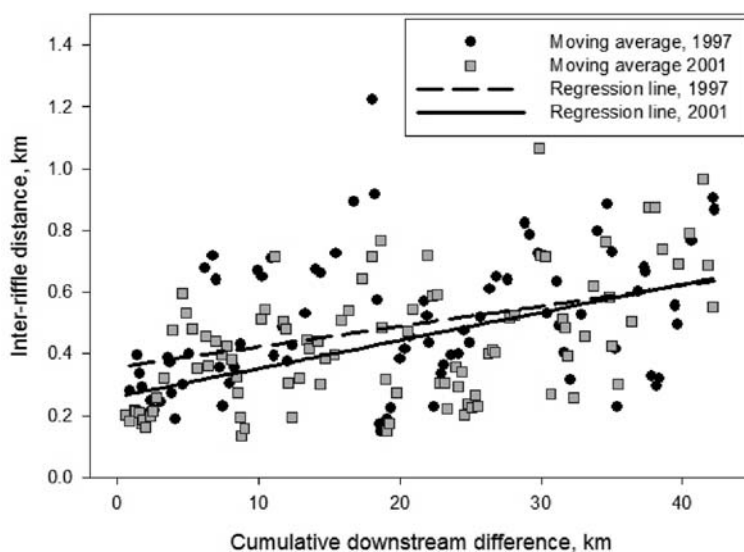


Figure 6. The distance between riffles, based on a moving average of three, for the lower section of Bayou Pierre, Copiah and Claiborne counties in 1997 and 2001. The starting point (km = 0) is just above the Mississippi Highway 18 bridge crossing (point A of Figure 1).

processed during the 2001 survey represented a narrower size range (24–47 mm SL) compared to the 1997 survey (20–48 mm SL), and in 1997 were more evenly distributed among all size classes (Figure 7). The majority of individuals processed during 2001 (79%) were between 30 and 36 mm SL.

Therefore, to further test for differences in age structure between upstream and downstream riffles, we compared our 1997 data from stage IV riffles to those of Knight & Ross (1992) for stage III riffles. Knight & Ross (1992) presented length-frequency distributions for samples taken from stage III in September 1986 and 1987 from several sites along Bayou Pierre and Foster Creek. There were no differences in length-frequency distributions of *E. rubrum* between September 1986 and 1987 (K–S  $Z_{(16)} = 0.708$ ,  $p = 0.699$ ). Again, the results do not show a difference in size structure between stage III and IV reaches [stage IV (1997) vs. stage III (1986), K–S  $Z_{(16)} = 0.884$ ,  $p = 0.415$ ; stage IV (1997) and stage III (1987), K–S  $Z_{(16)} = 0.707$ ,  $p = 0.699$ ].

Mass-length relationships (growth) or condition (size-adjusted mass) did not differ between the 1997 and 2001 surveys when all individuals were included ( $F_{(1,410)} = 3.130$ ,  $p = 0.078$ ; slopes equal

$F_{(1,410)} = 0.485$ ,  $p = 0.487$ ). To test for differences among erosional stages we only used Age I fish (27–33 mm SL), following Ross et al. (2001), to minimize age-related biases in growth and condition and to allow use of 1993–1994 data from Ross et al. (2001). The source–sink prediction of poorer growth and condition of fish in downstream vs. upstream riffles was not supported. Based on all Age I fish, there was no difference in slopes or size-adjusted mean mass among the three erosional stages ( $F_{(2,445)} = 1.705$ ,  $p = 0.183$ ; slopes equal  $F_{(2,443)} = 0.975$ ,  $p = 0.378$ ). In addition, there was no difference among erosional stages for size-adjusted mean mass in males ( $F_{(2,151)} = 0.772$ ,  $p = 0.464$ ; slopes equal  $F_{(2,149)} = 4.243$ ,  $p = 0.016$ ) or females ( $F_{(2,447)} = 1.947$ ,  $p = 0.144$ ; slopes equal  $F_{(2,445)} = 0.245$ ,  $p = 0.783$ ).

## Discussion

The propensity of aquatic organisms to drift, especially aquatic invertebrates, has been the subject of stream ecologists for many years (reviewed by Hynes 1970, Waters 1972, Müller 1974). Among fishes, the degree of downstream displacement or migration differs substantially as

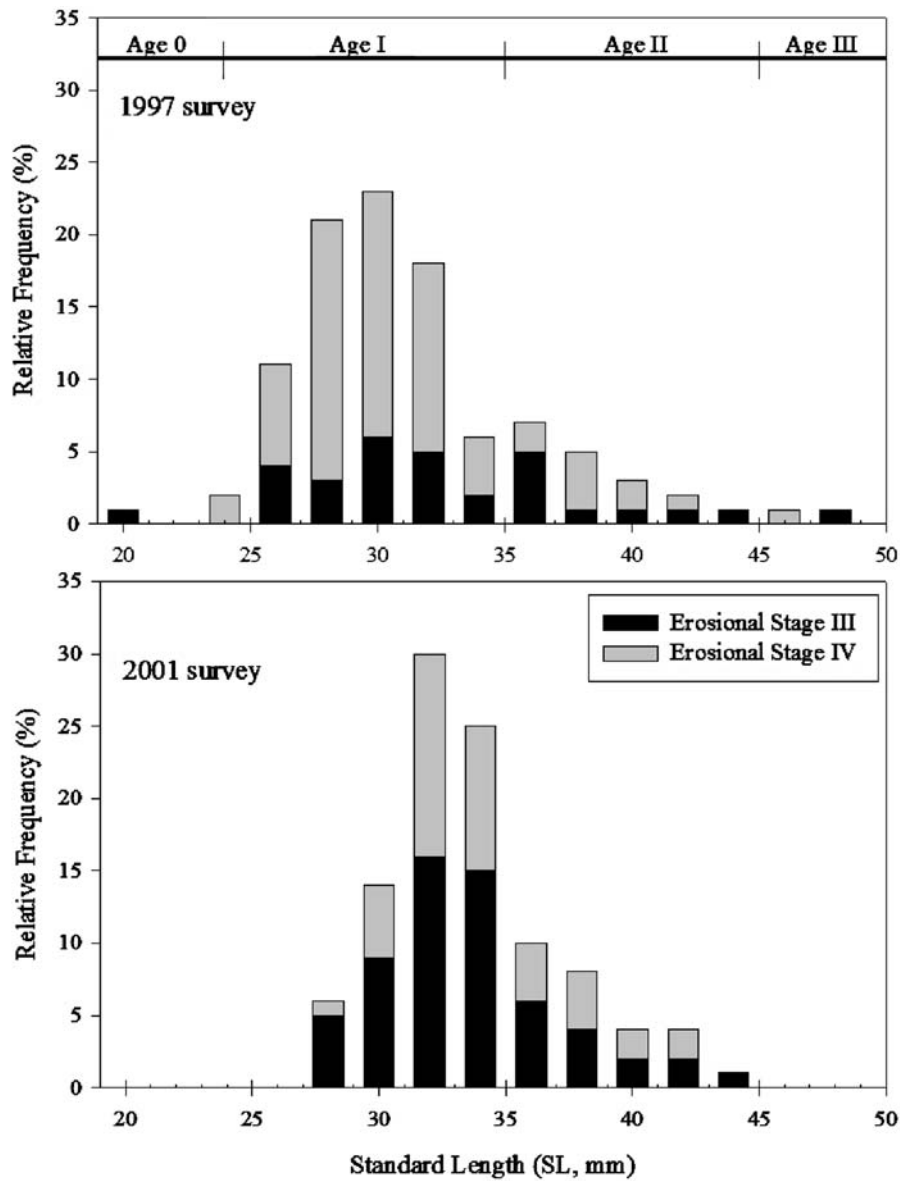


Figure 7. The age distribution of *Etheostoma rubrum* processed during the 1997 (upper panel) and 2001 (lower panel) sampling of the lower reach of Bayou Pierre. The location of the erosional stages is shown in Figure 1; estimated ages are based on Knight & Ross (1992).

each taxon (or suite of taxa) has evolved unique migratory behavior patterns dependent upon existing environmental conditions, the stage of migration in the life cycle (e.g., egg, larval, juvenile), and the mechanism of migration (e.g., passive, active) (Pavlov 1994). For percids, larvae of the commercially and recreationally important walleye, *Stizostedion vitreum*, and yellow perch,

*Perca flavescens*, exhibit substantial drift with greatest abundances occurring at night (Gale & Mohr 1978, Corbett & Powles 1986, Johnston et al. 1995). The occurrence of *Etheostoma* species in diel drift samples has been documented in several studies, with peak abundances typically at night from 2100 to 0300 h in both stream (Gale & Mohr 1978, Lathrop 1982, Brown & Armstrong

1985) and swamp habitats (Paller 1987). In Kentucky, Floyd et al. (1984) collected larval and juvenile *E. bellum* (subgenus *Nothonotus*) in light trap and seine samples but not in drift nets. However, during each sample period, Floyd et al. (1984) took their drift sample from only one station (#9) located just above a riffle-chute area. They operated the remaining gears (light trap, seine) in eight additional macrohabitats. They documented six species of darters from the study area with only one, *Percina caprodes*, represented in the drift samples, and then only by a few individuals. Because there was only one drift net and it was placed above the riffle, and we are unsure of what the upstream habitat resembled, it is not possible to determine the efficiency of the drift samples in documenting downstream displacement. Potentially, darters could have been spawned in the riffle area, but with the collecting device placed upstream of the riffle, the Floyd et al. (1984) study would have missed any downstream dispersal of larval darters. Scheidegger (1990) collected *E. jordani* (subgenus *Nothonotus*) in larval samples from two river systems in Alabama. Most (97.2%) *E. jordani* larvae were collected with a larval seine, although a few were collected with boat mounted push-nets. Push-nets are active collecting devices, capturing larvae drifting within the water column; however, because of the possibility that net turbulence might suspend otherwise demersal larvae, Scheidegger's work also does not unequivocally demonstrate larval drift in *Nothonotus*.

Our study is apparently the first to unequivocally report downstream displacement (drift) in a species of *Nothonotus*. Larval stages of *E. rubrum* occurred consistently in both cross-sectional and longitudinal drift nets throughout most of the study period. Drifting larvae were taken both downstream and upstream of riffles, and in the latter case the next upstream riffle was often several hundred meters distant. Most studies report that larval percids are more abundant in the drift at night, typically 2300–0300 h (cited above). In contrast, we did not find significant differences in drift over six 4 h time periods for *E. rubrum* or *Etheostoma* spp., and when we condensed the analysis to day–night differences, *E. rubrum* tended to be more abundant during the day.

Drift in fishes may be passive or active with younger or developmentally less mature life history stages more prone to enter drift passively because of their physical inability to resist stream currents (Pavlov 1994). Brown & Armstrong (1985) also contended that drift of most species of stream fishes was accidental or passive, but considered the occurrence to be related to chance encounters with strong currents during feeding. They reported that few prolarvae (yolk-sac larvae) occurred in drift samples whereas postlarvae (yolk-sac absorbed) apparently entered the drift as their yolk sacs became depleted and exogenous feeding had begun. In contrast, Scheidegger (1990) noted that early protolarvae (yolk-sac larvae) of percids were captured in greater numbers in drift nets whereas an increase in late mesolarvae and metalarvae (yolk-sac absorbed) in larval seine samples was accompanied by a decrease in the drift. Our data follow those of Scheidegger (1990) in that *E. rubrum* captured by drift nets were either protolarvae or early mesolarvae (i.e., yolk-sac larvae). Because we failed to collect metalarval or juvenile life history stages with our sampling gears, *E. rubrum* larvae likely settle out of the drift as they reach later developmental stages.

Protolarvae and mesolarvae of *E. rubrum* were common, although not abundant, components of the drift. Because they do occur in the drift, the downstream dispersal of larval *E. rubrum* is highly probable; however, the overall distance of downstream dispersal is problematic. There is very little information in the literature on how far larval fishes may drift, particularly percids. While assessing the efficiency of drift samples for estimating *Stizostedion vitreum* larval abundances, Franzin & Harbicht (1992) conducted experiments in which they released many hatchery-reared larvae (65 000–311 000) at varying distances from downstream drift nets (30 m–5 km). Mean recapture efficiency (observed catch/expected catch) was rather high for nets sampled 30, 100 and 300 m downstream of release points (95% CI: 43–474%), whereas recapture efficiency for nets 1 and 5 km downstream of release points was relatively low (95% CI: 3.3–7.2%). Although *E. rubrum* and *Stizostedion* are both percids, they are on different evolutionary trajectories. Nonetheless, these results suggest that the potential for *E. rubrum*

larvae to drift up to 300 m is probable but that distances of 1–5 km are not likely.

The downstream sampling showed that *E. rubrum* continues to persist in the lower reaches of Bayou Pierre between Mississippi Highway 18 and the confluence with Little Bayou Pierre. The prediction, from a source–sink hypothesis, that age structure was truncated in lower reach populations was not supported. There was no difference in inferred age structure of *E. rubrum* between stages III and IV, with YOY to Age III fish represented. This suggests that populations of *E. rubrum* in the lower reaches of Bayou Pierre are self-sustaining.

Condition of *E. rubrum*, as indicated by mass–length relationships, was also invariant between upstream and downstream riffles. This is contrary to the second prediction of the source–sink hypothesis that habitat quality would be lowered in downstream riffles and would be reflected by poorer condition. It may be, however, that even though fish condition did not differ, downstream riffles might support smaller populations of *E. rubrum*. We did not determine actual densities of local populations of *E. rubrum* in this study.

Ross et al. (1992) suggested, based on the relative abundance of juvenile vs. adult *E. rubrum* in the downstream section of Bayou Pierre, that there was the possibility of downstream transport of eggs or larvae, followed by upstream migration. Our data comparing age structure between stages III and IV would seem appropriate to test this hypothesis even though few YOY were collected. If extensive downstream transport followed by upstream movement were occurring, then riffles in stage IV should have supported a higher proportion of younger fish (Age I) than stage III. Because there was no difference in age structure for similar times of the year between the two stages, the hypothesis of extensive downstream transport followed by upstream movement is not supported, at least in terms of long-distance (e.g., >1 km) upstream migration. However, because we have shown that larvae are drifting, there is the distinct possibility of downstream transport followed by upstream movement, but on a smaller spatial scale (e.g., <1 km).

The trend for greater inter-riffle distances in the lower reaches of Bayou Pierre, coupled with the knowledge of some degree of larval drift of

*E. rubrum*, suggests that the probability of colonization of a riffle should decrease with distance downstream. Recolonization of newly formed riffles in upstream areas (e.g., stages II–III), following riffle loss due to sedimentation or changes in channel morphology, should occur more rapidly than those in downstream (stage IV) regions. Without knowing the extent of movement of juvenile and adult fish, such colonization would likely involve both larval as well as older life history stages. Recruitment of *E. rubrum* to riffles in the lower reaches of Bayou Pierre (i.e., from just above to below MS Hwy. 61), would likely take longer, as colonization would necessarily occur from more distant upstream sites.

If drifting in *E. rubrum* is a distinct adaptation for colonization, then genetic integrity of each riffle should remain homogenous. Genetic homogeneity of *E. rubrum* is supported by Wood's (1996) allozyme data on samples from Bayou Pierre and Foster Creek. Consequently, it may be appropriate to consider riffles as islands occupied by *E. rubrum*, with the islands populations connected by periodic gene flow maintained by the annual drift cycle of larvae and an unknown degree of adult movement (e.g., *E. rubrum* may exist as a metapopulation). Loss of riffle habitat, and thus loss of component populations, would reduce the probability of gene flow, thus weakening the overall metapopulation. Such losses are perhaps more severe downstream, where inter-riffle distances are greatest.

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