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Ichthyofaunal and Habitat Associations of Disjunct Populations of Southern Redbelly Dace. *Phoxinus erythrogaster* (Teleostei: Cyprinidae) in Mississippi

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ABSTRACT.—Twenty-two field sites in W-central Mississippi were surveyed for southern redbelly dace *Phoxinus erythrogaster* to characterize habitat and ichthyofaunal associations of these 'endangered' disjunct populations. *Phoxinus erythrogaster* occurred at only six sites. Data assessed similarity among all sites and described microhabitat associations of *P. erythrogaster*. Five species, including *Semotilus atromaculatus*, *Camptostoma anomalum*, *Etheostoma whipplei*, *P. erythrogaster* and *Pimephales notatus*, comprised 95% of the total number of individuals collected at *P. erythrogaster* sites. Standardized abundance (number per seine haul) for *S. atromaculatus* was consistently high among all *P. erythrogaster* sites, whereas standardized abundance for *C. anomalum*, *P. erythrogaster* and *P. notatus* varied from site to site. Increased standardized abundance of *P. erythrogaster* was inversely related to abundances of *C. anomalum* and *P. notatus* and was highest in the absence of *C. anomalum* and *P. notatus*. Thus competition among *C. anomalum*, *P. erythrogaster* and *P. notatus* may be linked to the limited occurrence of *P. erythrogaster* in W-central Mississippi. A UPGMA cluster analysis of ichthyofaunal composition (chord distance) showed high similarity among the six sites where *P. erythrogaster* was present. These sites were typically characterized as narrow meandering streams with gravel, pebble and sand substrata, slow-flowing pools with clear cool (22 C) water and steep banks. A discriminant function analysis indicated that the presence of *P. erythrogaster* is associated with stream reaches with high proportions of gravel, detritus, snag, pebble, small cobble and small boulder (Canonical $R = 0.73$, $P = 0.018$). A test of the reliability of the predictive model resulted in 87% of the cases being correctly classified ($P < 0.01$). Declining habitat quality due to erosion and increased urban development was evident at a number of sites including two historic localities where *P. erythrogaster* no longer occurs. *Phoxinus erythrogaster* abundance was low along degraded stream reaches and typically higher in areas where habitat has been less impacted. Clustering of sites where *P. erythrogaster* was present, based on habitat similarity (chord distance), was not as strong as similarity based on ichthyofaunal composition. There was significant congruence between the two dendrogram matrices (Mantel $z = 314.69$, $P = 0.014$) but the relationship between corresponding similarity values was low ($r_{cs} = 0.334$). Thus, the ability to predict sites similar in ichthyofaunal composition based on habitat similarity was low. This suggests that although specific habitat features are important to *P. erythrogaster*, additional factors such as declining habitat quality and interspecific competition may be influencing the occurrence of *P. erythrogaster* in W-central Mississippi.

INTRODUCTION

The southern redbelly dace *Phoxinus erythrogaster* is a colorful, small to medium-sized minnow (55 to 65 mm SL; Starnes and Starnes, 1980) that is widely distributed within the upper Mississippi River Valley. It is generally abundant in upland streams of the Great Lakes and Mississippi River basins from Minnesota to western New York, S to the Ozark highlands of Arkansas and Oklahoma and the lower Tennessee River drainage of Tennessee, Alabama and Mississippi (Starnes and Starnes, 1980). Additional disjunct populations occur in Arkansas, Colorado, Kansas, Minnesota, Mississippi, New Mexico and Oklahoma (Miller and

Robison, 1973; Page and Burr, 1991) with disjunct populations in western Mississippi being the most southern (Hemphill, 1957; Cashner *et al.*, 1979). These localized Mississippi populations which are considered 'endangered' by the Mississippi Department of Wildlife, Fisheries and Parks (1994) occur in the Lower Mississippi, Tallahatchie and Yazoo river systems in Tallahatchie, Warren and Wilkinson counties (Ross and Brenneman, 1991).

We surveyed the populations of *Phoxinus erythrogaster* in Warren and Tallahatchie counties (Slack *et al.*, 1995), and herein describe the habitat and ichthyofaunal associations of these populations. Specifically, we asked whether *P. erythrogaster* was associated with particular ichthyofaunal components and/or specific habitat characteristics. Also we wanted to determine habitat parameters that might be useful in describing favorable habitat for these disjunct populations. Knowledge of faunal and habitat associations would be beneficial for conservation and management of these populations.

METHODS

Sampling.—Twenty-two sites in Tallahatchie (2 sites) and Warren counties [Bliss Creek (7 sites), Hatcher Bayou (7) and Skillikalia Bayou (6)] were sampled from July to September 1994. Included among these sites were seven historic localities for *Phoxinus erythrogaster* noted from collection records and literature references. All sampling occurred along the Loess Hills region that forms the eastern border of the Mississippi Alluvial Plain (Cross *et al.*, 1974). Primary sampling efforts focused on 100-m stream reaches extending upstream and downstream from each sampling site, *e.g.*, bridge crossing. Block nets were used at 14 sites and were placed at the upstream and downstream border of each 100-m sample reach to prevent fishes from either being permanently dislodged from specific habitats or from leaving the sampling area. Three, 10-m long subreaches were randomly chosen within each 100-m sample reach, and each subreach was isolated with block nets before sampling. Sampling within each subreach consisted of 10 to 15 seine hauls. After sampling the three subreaches, we seined the remaining portion of the 100-m sample reach to determine the presence of additional *P. erythrogaster*. Representative voucher collections from all subreach samples were preserved in the field and returned to USM for enumeration and identification. All species except *P. erythrogaster* were preserved. No voucher material was preserved from the 100-m generalized samples. We were unable to use block nets at eight sites; therefore, we simply designated a length of stream (50–100 m) and sampling consisted of general seining through all available macrohabitats without the designation of subreaches. These sampling efforts were kept consistent with 10–20 seine hauls per reach. To ensure unbiased comparisons among sites, fish abundance at each site was standardized as the number of individuals of each species per seine haul (standardized abundance). All sites were sampled with a 1.8 × 3.1 m seine with 3.2 mm Ace mesh (6 × 10' with 1/8" mesh). All material was curated and deposited in the USM Museum of Ichthyology.

We characterized habitat only at those sites where subreaches were sampled [14 sites: Tallahatchie Co. (2 sites), Bliss Creek (7), Hatcher Bayou (1) and Skillikalia Bayou (4)]. Habitat was characterized by designating a representative transect across each sampled subreach (3 per 100 m). Along the transect we recorded stream width and constructed a depth profile at 0.5-m intervals. Substratum composition (%) was visually estimated within each subreach following a modified Wentworth scale (Cummins, 1962). Substratum categories were: (1) hard clay (soapstone); (2) soft clay (loose); (3) silt; (4) mud; (5) sand (1–8 mm diam); (6) gravel (8–16 mm diam); (7) pebble (16–32 mm diam); (8) small cobble (32–64 mm diam); (9) large cobble (64–256 mm diam); (10) small boulder (256–320 mm diam), and (11) large boulder/rip-rap (> 320 mm diam). Additional categories included (12) detritus, (13) aquatic vegetation, (14) snag and (15) concrete (bridge abutment). Water

temperature (C) was measured at each site, and stream order was determined from 1:24,000 USGS topographic maps (Horton, 1945; Strahler, 1957).

Analyses.—We compared ichthyofaunal and habitat similarity among sites using an unweighted pair group average method (UPGMA) cluster analysis (Pielou, 1984). Similarity was calculated as chord distance because it is considered more appropriate for species abundance data than Euclidean distance (Ludwig and Reynolds, 1988). Chord distance places greater importance on the relative proportion of individual categories in the sampling units (species or habitats) while Euclidean distance is more strongly influenced by the more abundant or dominant category (Gauch, 1982; Legendre and Legendre, 1983). Sites with the greatest similarity entered the analysis first, with less similar sites added sequentially, *i.e.*, nonrandom input order. A matrix correlation coefficient (r_{cs}) (Sokal and Rohlf, 1962) was computed for each similarity matrix and the resulting dendrogram (cophenetic values; Sneath and Sokal, 1973). The coefficient depicts the linear relationship between corresponding elements of two matrices and provides a measure of agreement between the original similarity matrix and the classification resulting from the cluster analysis. Values for r_{cs} range 0 to 1 with high values indicating good retention of the relationship among the original similarity values by the cluster analysis.

The ichthyofaunal data matrix included all species and the standardized abundance for each species at each site. Data were assessed for violation of statistical assumptions and as not being in need of transformation. Habitat data were used in two separate analyses, habitat similarity among sites and microhabitat association of *Phoxinus erythrogaster*. For the first analysis, the habitat data matrix was computed using mean habitat values for each of the 14 sites based on all subreach transect measurements (three or six per site). The following variables were recorded for each site: mean proportion of each substratum category, water temperature (TEMP), mean stream width (WIDTH), standard deviation of stream width (WSTD), coefficient of variation of stream width (WCV), mean stream depth (DEPTH), standard deviation of stream depth (DSTD), coefficient of variation of stream depth (DCV) and stream order (ORDER). Habitat variables were assessed for violation of statistical assumptions before the analysis, and were transformed to improve normality, linearity and homogeneity of variances. Substratum variables were arcsine transformed ($\sqrt{\text{variable}}$; Winer *et al.*, 1991) and the remaining variables were \log_{10} transformed except for stream width and stream order. Stream width departed from normality when transformed and stream order was treated as a categorical variable (values ranged 1 to 3); therefore, neither was transformed for the analysis.

In the second analysis we used a linear discriminant function analysis (CVA, CANOCO 3.12; ter Braak, 1991) on all subreach transect measurements (three or six per site, 60 total) to describe the association between the presence of *Phoxinus erythrogaster* and the corresponding suite of habitat variables. Presence/absence of *P. erythrogaster* at each subreach and all habitat variables described in the cluster analysis were used with the exception of standard deviation and coefficient of variation of stream width. Stream width was reported as the actual width for each transect. Data were assessed for violation of assumptions and transformed as described previously. All habitat variables were retained in the data matrix and all were included in the computation of the discriminant function, *i.e.*, no stepwise or forward selection of variables. Significance of the canonical axis was tested by Monte Carlo permutations (CANOCO 3.12; ter Braak, 1991).

Ideally, to test the discriminatory ability of the predictive model one would randomly divide the data set in half, use one-half to build the model and cross-validate the model with the remaining cases. This procedure is recommended to reduce bias and to test the generalizability of the model (Tabachnick and Fidell, 1989). Unfortunately, overall group

TABLE 1.—Numerically abundant species collected from 22 sites sampled for *Phoxinus erythrogaster*. Column 1 includes overall relative abundance (%) of the 15 numerically most abundant species based on all sites; column 2 lists the relative abundance of the 12 species collected at sites where *P. erythrogaster* was present. Species are ranked according to overall relative abundance

Species	Overall	Dace sites	Species	Overall	Dace sites
<i>Semotilus atromaculatus</i>	29	53	<i>Fundulus notatus</i>	2	
<i>Campostoma anomalum</i>	11	18	<i>Lepomis macrochirus</i>	2	
<i>Pimephales notatus</i>	11	6	<i>Hybognathus nuchalis</i>	2	
<i>Cyprinella lutrensis</i>	11	1	<i>Luxilus chrysocephalus</i>	1	<1
<i>Etheostoma caeruleum</i>	8		<i>Lepomis megalotis</i>	<1	
<i>E. whipplei</i>	6	11	<i>Etheostoma parvipinne</i>		<1
<i>Gambusia affinis</i>	6	3	<i>Aphredoderus sayanus</i>		<1
<i>Phoxinus erythrogaster</i>	4	7	<i>Etheostoma gracile</i>		<1
<i>Fundulus olivaceus</i>	2		<i>Ameiurus natalis</i>		<1
<i>Lepomis cyanellus</i>	2				

sample size must be large enough so that the reduction of the data set allows one to build a reliable model. We considered group size for the 60 characterized transects (19 with *Phoxinus erythrogaster* present, 41 absent) too small to conduct this procedure and still make an adequate statement about the model. Consequently we built the model with all the data in hand and assessed the predictability of the classification model by comparing predicted group membership against actual group membership with prior probabilities based on group size (DISCRIM SPSS[®] 2.1; SPSS, 1985).

To assess the importance of habitat in explaining the occurrence of *Phoxinus erythrogaster* among sites, we compared the dendrogram matrices (cophenetic values) of ichthyofaunal and habitat similarity among the 14 sites that habitat was characterized using a Mantel test (Mantel, 1967). Significance of the test was determined by comparing the actual test statistic to the distribution of test statistics calculated from 9999 random permutations of the first matrix (Rohlf, 1992). Congruence between the two matrices indicates that sites similar in ichthyofaunal composition are also similar in habitat, thereby relating the importance of habitat to the local occurrence of *P. erythrogaster*. The lack of congruence, although it does not dismiss the importance of habitat to *P. erythrogaster*, suggests that additional factors may be responsible for explaining the occurrence of *P. erythrogaster*.

RESULTS

Species occurrence.—Combined collections from the 22 sites yielded 2932 individuals representing 32 species and eight families. One hundred forty-seven *Phoxinus erythrogaster* were collected at six sites [Tallahatchie Co. (1 site); Warren Co.: Bliss Creek (3); Skillikalia Bayou (2)]. Total number of species per site varied from three to 16 at all sites and five to nine at *P. erythrogaster* sites. Absolute abundance of *P. erythrogaster* was typically low, ranging from 7–40 individuals per site.

For all sites combined, the 15 numerically dominant species comprised 97% of the total number of individuals collected. The five numerically dominant species comprised 70% of the individuals, including *Semotilus atromaculatus* (29%), *Campostoma anomalum* (11%), *Pimephales notatus* (11%), *Cyprinella lutrensis* (11%) and *Etheostoma caeruleum* (8%). *Phoxinus erythrogaster* ranked eighth in overall relative abundance (4%) (Table 1). Only 12 species occurred at the six sites at which *P. erythrogaster* were collected. At these sites, the

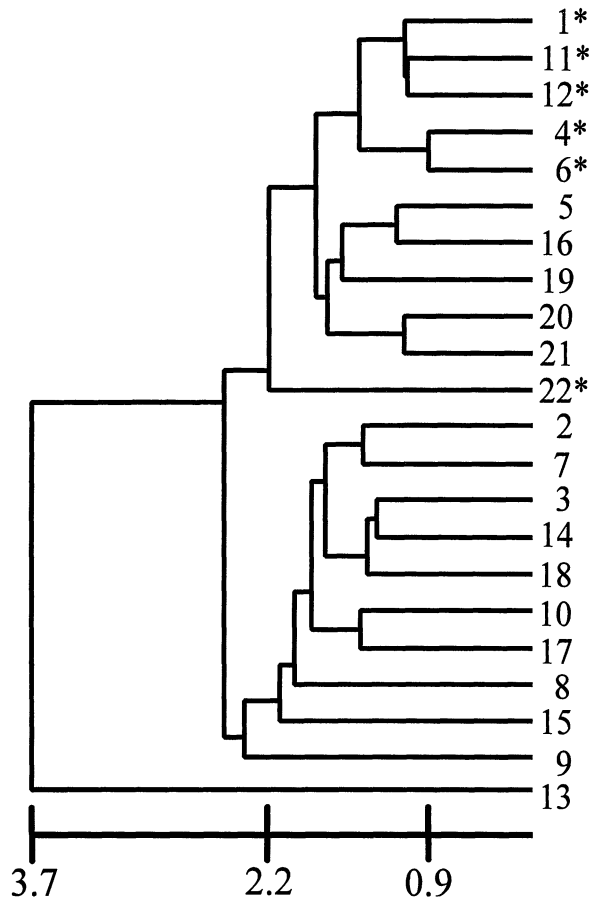


FIG. 1.—Dendrogram representing ichthyofaunal similarity (chord distance) among 22 sites sampled in west-central Mississippi for *Phoxinus erythrogaster*. An asterisk indicates sites where *P. erythrogaster* were present. The matrix correlation coefficient (r_{cs}) = 0.862

five numerically dominant species constituted approximately 95% of the total number of individuals collected. Again, *S. atromaculatus* ranked first (53%) followed by *C. anomalum* (18%), *Etheostoma whipplei* (11%), *P. erythrogaster* (7%) and *Pimephales notatus* (6%).

Five of the six sites at which *Phoxinus erythrogaster* occurred had similar fish assemblages (Fig. 1) while the remaining *P. erythrogaster* site (Site 22, Murphy Branch) was isolated geographically (Tallahatchie Co.) and was the least similar to the other *P. erythrogaster* sites. Standardized abundance (number per seine haul) for *S. atromaculatus* was consistently high among all *P. erythrogaster* sites while standardized abundance for the remaining species varied from site to site (Fig. 2). Increased standardized abundance of *P. erythrogaster* was inversely related to abundances of *C. anomalum* ($r = -0.878$, $P = 0.021$) and *Pimephales notatus* ($r = -0.761$, $P = 0.079$). Standardized abundance of *Phoxinus erythrogaster* was highest at Site 22, where *C. anomalum* and *Pimephales notatus* were not collected.

Habitat.—Stream reaches where *Phoxinus erythrogaster* occurred were typically covered

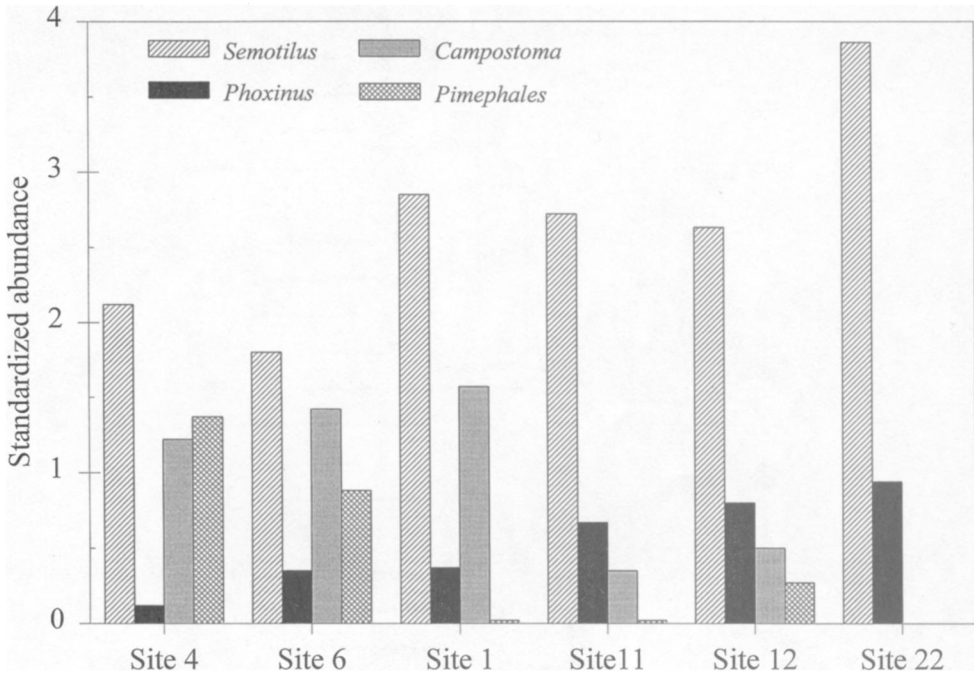


FIG. 2.—Standardized abundance (catch per seine haul) of dominant cyprinids present at *Phoxinus erythrogaster* sites. The order of sites along the x-axis is based on increasing standardized abundance of *P. erythrogaster*

with a dense riparian canopy (pers. observ., WTS). Common riparian species included *Platanus occidentalis*, *Liriodendron tulipifera*, *Acer negundo* and various species of *Robinia*, *Gleditsia*, *Quercus* and *Fraxinus*. Streams were typically narrow, meandering primarily over gravel, pebble and sand substrata. Plunge pools and chutes at the base of shallow riffles and runs were common along undercut clay banks. Sites where *Phoxinus erythrogaster* were more abundant typically had several long, slow-flowing pools usually with clear, cool water (range 17 to 24 C; \bar{x} = 22 C). Streams were bordered by steep banks and the stream bed was typically well-incised into the loess deposits. The distance from the stream bed to the terrace above the bank was usually 1.5 to 2.0 m. Streamside vegetation often included dense patches of horsetail (*Equisetum hyemale*) and bamboo (*Arundinaria gigantea*). Substrata were similar among all sites (Fig. 3). Sand was the most common substratum with a mean of 34% at sites where *P. erythrogaster* was present and 37% at sites where absent. Sites where *P. erythrogaster* occurred generally had increased proportions of gravel, pebble, detritus and snag, whereas sites where *Phoxinus erythrogaster* was absent had greater amounts of clay (hard and soft), silt and mud. However, only proportions of soft clay ($t_{(1,27)} = 2.046$, $P = 0.050$), mud ($t_{(1,36)} = 3.426$, $P = 0.002$), gravel ($t_{(1,55)} = 2.807$, $P = 0.007$) and pebble ($t_{(1,57)} = 2.873$, $P = 0.003$) were significantly different between sites where *P. erythrogaster* was present and absent. Although large boulder (rip-rap) occurred at *P. erythrogaster* sites, *P. erythrogaster* was never collected in association with this introduced substratum. No significant difference was found in the number of substratum categories between sites where *P.*

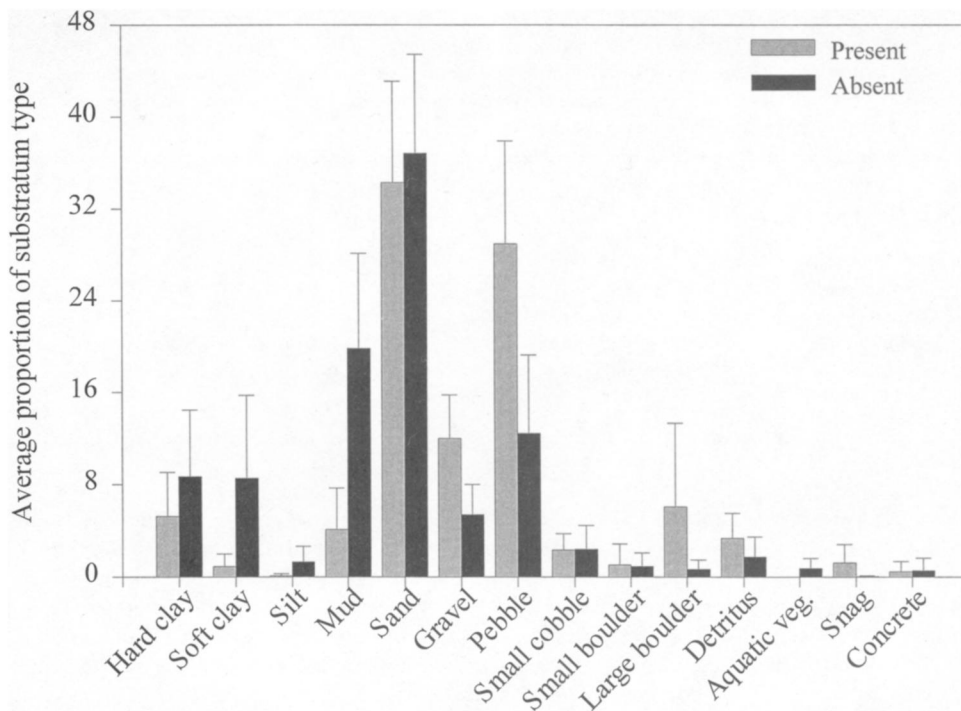


FIG. 3.—Average proportion of substratum types present at sites sampled for *Phoxinus erythrogaster*. Light bars indicate sites where *P. erythrogaster* was present; dark bars indicate sites where *P. erythrogaster* was absent. Vertical bars represent 95% confidence intervals. See methods for description of substrata

erythrogaster was present ($\bar{x} = 4.3$, $SD = 1.2$) and absent ($\bar{x} = 4.4$, $SD = 1.2$) (Mann-Whitney $U_{(27,33)} = 470.5$, $P = 0.716$).

The discriminant function analysis on microhabitat measurements (60 transects: 19 with *Phoxinus erythrogaster* present, 41 absent) indicates a significant relationship between *P. erythrogaster* presence/absence and the environmental axis—a reflection of the measured habitat variables (Canonical $R = 0.73$). The correlation between the environmental and species axes accounted for 53% of the variance in the habitat data. The Monte Carlo test was computed with 9999 permutations (exact permutations = 8×10^{81}) and the canonical axis was significant with only 180 of the total permutations greater than the computed test statistic, $F = 44.38$ ($P = 0.018$). Correlations of habitat variables on the environmental axis (Table 2) indicate that presence of *P. erythrogaster* is associated with high proportions of gravel, detritus, snag, pebble, small cobble and small boulder while transects with high amounts of mud, large boulder (rip-rap), soft clay, aquatic vegetation and silt lacked *P. erythrogaster*. Additionally, *P. erythrogaster* presence was associated with decreased water temperature ($r = -0.183$) and lower stream order ($r = -0.207$) (Table 2).

Overall, 87% of the cases were classified correctly; 90% were classified correctly for transects with *Phoxinus erythrogaster* absent and 79% correct with *P. erythrogaster* present. Four transects from each group were misclassified. Of the four misclassifications for *P. erythrogaster* absent, two of the transects were actually at sites where *P. erythrogaster* were collected although not in the subreach of that specific transect. We interpret this as a case of fish

TABLE 2.—Correlations of habitat variables on the canonical axis determined from a linear discriminant function analysis. Variables are listed in order of the correlation value. Variables with largest absolute values are considered to be of the greatest importance in delineating between *Phoxinus erythrogaster* presence/absence. Positive correlations are associated with *P. erythrogaster* presence. See methods for description of variables

Gravel	0.306	Sand	-0.057
Detritus	0.299	Width	-0.094
Snag	0.244	Depth	-0.098
Pebble	0.243	Silt	-0.115
Small cobble	0.149	Aquatic vegetation	-0.154
Small boulder	0.100	Soft clay	-0.169
Concrete	0.073	Water temperature	-0.183
CV of depth	0.027	Large boulder	-0.192
STD of depth	-0.014	Stream order	-0.207
Hard clay	-0.036	Mud	-0.311

movement along a favorable stream reach rather than an actual case of habitat misclassification. Based on group size (19 present, 41 absent) the total number of cases that would be correctly classified by chance is 56.7%. Our classification of 87% was significantly more than expected by chance ($\chi^2 = 14.22$, $P < 0.01$). A more specific test designed for determining chance-corrected classifications of discriminatory analyses is Cohen's K (Titus *et al.*, 1984), which is particularly useful with unequal sample sizes. For our data, $K = 0.694$ which corresponds to a 69.4% correct classification rate better than expected by chance ($z = 3.809$, $P < 0.001$).

The cluster analysis of the 14 sites where habitat was characterized reflects the position of the sites along a specific stream in terms of gradient, channel characteristics and substrata composition (Fig. 4a). It does not support the notion of habitat homogeneity within a specific stream system, where sites within the same system would be more similar to each other than to sites in other systems. There is not a strong grouping of *Phoxinus erythrogaster* sites based on habitat similarity, although *P. erythrogaster* were typically present at sites located along headwater reaches or in small tributaries. Sites 11, 12 and 22 show the greatest habitat similarity among *P. erythrogaster* sites, while Sites 1 and 6 are more similar to sites where *P. erythrogaster* were absent. In addition, Sites 1 and 6 show greater similarity to sites where *P. erythrogaster* were absent (5, 7, 9 and 10) than to the remaining *P. erythrogaster* sites. In contrast, similarity among the 14 sites based on ichthyofaunal composition illustrates strong grouping of *P. erythrogaster* sites (Fig. 4b). As in Figure 1, five of the six *P. erythrogaster* sites are more similar to each other than to the remaining sites. Site 22, as noted earlier, was isolated geographically and was least similar to the other *P. erythrogaster* sites. The comparison of dendrogram matrices for ichthyofaunal and habitat similarity indicates significant congruence (Mantel $z = 314.69$, $P = 0.014$) but the relationship between corresponding elements of the two matrices is low ($r_{cs} = 0.334$).

DISCUSSION

The link between abundance of *Phoxinus erythrogaster* and the availability of favorable habitat has been described by several authors. In Wisconsin, Becker (1983) described *P. erythrogaster* as abundant in small streams typically <6.0 m wide. Water depth ranged from 0.1 to 1.5 m, substrata were primarily gravel, rubble, silt and sand, and vegetation was sparse to absent in stream reaches where *P. erythrogaster* occurred. The Kentucky study site de-

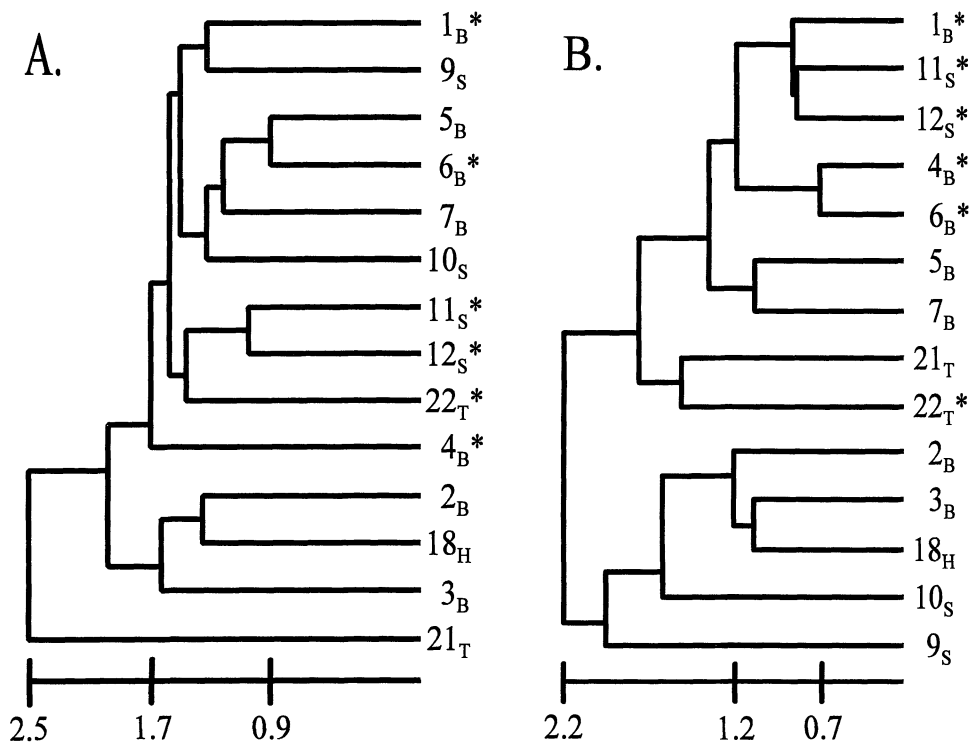


FIG. 4.—Dendrograms representing similarity (chord distance) among 14 sites sampled for *Phoxinus erythrogaster* (A: habitat; B: ichthyofauna). An asterisk indicates sites where *P. erythrogaster* was present. Subscripts indicate water body or system where the site was located: B = Bliss Creek, H = Hatcher Bayou, S = Skillikalia Bayou and T = Tallahatchie Co. The matrix correlation coefficient (r_{cs}) for habitat = 0.817; ichthyofauna r_{cs} = 0.799

scribed by Settles and Hoyt (1976, 1978) ranged from 0.9 to 3.7 m wide, numerous riffles often separated long pools of moving water (0.3–0.6 m deep), and undercut banks were common. Similarly, Trautman (1981) stated that in Ohio, high abundance of *P. erythrogaster* was typical in small, clear streams that flowed between wooded banks. These reaches also contained long pools of moving water along undercut banks overhung by vegetation.

Felley and Hill (1983), using a more analytical approach, addressed seasonal habitat associations of cyprinids in the Illinois River, Oklahoma. In their study, *Phoxinus erythrogaster* occurred in narrow (3–4 m wide) spring-influenced headwater reaches (2nd order) with clear, cool water (ca. 2 °C lower than drainage mean). *Phoxinus erythrogaster* were captured in shallow reaches (0.49–0.68 m deep) over gravel substrata. Current velocity varied seasonally, with *P. erythrogaster* associated with velocities of 0.14 to 0.19 m/sec from spring to autumn and 0.08 m/sec during the winter. *Phoxinus erythrogaster* were significantly associated with debris (leaves and sticks on the bottom) during all seasons, but only variably associated with emergent aquatic vegetation and cover. The association with emergent vegetation was greatest during summer and autumn while the association with cover was greatest during the autumn and winter. We found *P. erythrogaster* were similarly significantly associated with low order, headwater reaches in clear, cool water over gravel, pebble, detritus

and snag substrata. We have no quantitative data on current velocity, but *P. erythrogaster* typically occurred in reaches with flowing water, especially in chutes along undercut banks at the base of pools or shallow runs. McNeely (1987) examined niche relationships among seven cyprinids, including *Camptostoma anomalum*, *Semotilus atromaculatus* and *P. erythrogaster*, in Spring Creek, a Neosho River tributary in NE Oklahoma. *Phoxinus erythrogaster* were more abundant in shallow areas of the stream (\bar{x} depth = 0.4 m, SD = 0.18), occurring over gravel, cobble and rubble substrata. These substrata correspond to our gravel, pebble, small cobble and large cobble categories. Among the seven cyprinids studied, *P. erythrogaster* and *S. atromaculatus* were associated with sparse aquatic vegetation, and were more abundant near the stream edge than midstream. *Phoxinus erythrogaster* occurred mainly in stream velocities ranging 0.05 to 0.20 m/sec.

Although these comparisons provide no direct quantitative evidence, they do indicate that *Phoxinus erythrogaster* of western Mississippi populations occur in habitats that are similar to those described for other populations. The results from our discriminant function analysis strongly supports this contention, as local *P. erythrogaster* occurrence is linked to specific habitat features (stream reaches with high proportions of gravel, detritus, snag, pebble, small cobble and small boulder). Similarly, *P. erythrogaster* abundance at any site was influenced by habitat quality. Habitat quality varied from site to site in our study and the impact of local disturbances, such as erosion, headcutting and alterations due to highway construction, have affected a number of sites. Along degraded reaches (Sites 1 and 4) absolute abundance of *P. erythrogaster* was low. At areas where habitat was less disturbed, such as Sites 11 and 22, absolute abundance of *P. erythrogaster* was higher. The direct result of erosion is increased sediment loads in the neighboring watersheds (Smith and Patrick, 1991). Sedimentation and increased siltation of streams has been linked to declines in aquatic biodiversity, as indicator or intolerant species are quickly affected (Berkman and Rabeni, 1987; Karr and Dudley, 1981). Species of *Phoxinus* are known to be sensitive to perturbations with increased siltation being the major factor linked to declining abundances of *P. cumberlandensis* (Starnes and Starnes, 1981) and *P. tennesseensis* (Burkhead and Jenkins, 1991).

Ichthyofaunal composition for communities containing *Phoxinus erythrogaster* has been reported by a number of authors (Table 3). Cashner *et al.* (1979) reported a species composition similar to ours during a previous survey of Bliss Creek, noting 78% of total abundance was attributed to *Semotilus atromaculatus*, *Camptostoma anomalum* and *Pimephales notatus*. In contrast, their survey of Clark Creek in Wilkinson County indicated *S. atromaculatus*, *C. anomalum* and *P. notatus* accounted for only 37% of total abundance. McNeely (1986) reported *S. atromaculatus* and *C. anomalum* represented 15% of the total abundance in an Oklahoma Ozark stream. *Pimephales notatus* was not present at McNeely's sites but a herbivorous counterpart, *Notropis nubilis*, was present and comprised 13% of the total abundance. Becker (1983) provided data on the relative abundance of *Phoxinus erythrogaster* in Wisconsin as well as associated species; however, data were limited to only a few collections from a single stream. *Phoxinus erythrogaster* was the most abundant species with *C. anomalum*, *S. atromaculatus* and *Pimephales notatus* comprising only 39% of the total abundance. The observation that ichthyofaunal composition differs among these communities is no surprise because each community includes a number of species that are unique to that specific region. However, these comparisons illustrate general ichthyofaunal similarity when considering the presence of species common (shared) among these communities, in particular the presence of *C. anomalum*, *S. atromaculatus*, *P. notatus* and *Phoxinus erythrogaster*.

From these comparisons we make two basic conclusions. First, the occurrence of *Phoxinus erythrogaster* among our sites is linked to specific habitat features which are similar to those described for other populations. Also, *P. erythrogaster* abundance may be influenced by

TABLE 3.—Relative abundance (%) of *Phoxinus erythrogaster* and associated ichthyofauna reported from other studies

Location	Total species	Number of cyprinids	Relative abundance				Study
			<i>Semotilus atromaculatus</i>	<i>Camptostoma anomalum</i>	<i>Pimephales notatus</i>	<i>Phoxinus erythrogaster</i>	
Bliss Creek, MS	16	7	31	30	17	2	Cashner <i>et al.</i> (1979)
Clark Creek, MS	28	14	23	12	2	not provided	Cashner <i>et al.</i> (1979)
Spring Creek, OK	27	8	4	11	not present	4	McNeely (1986)
Bacon Creek, WS	13	9	4	33	2	35	Becker (1983)
<i>P. erythrogaster</i> sites (6)	12	5	53	18	6	7	present study

habitat quality. Absolute abundance of *P. erythrogaster* was low along reaches with degraded habitat while areas where habitat was less disturbed usually had higher absolute abundances. Secondly, the ichthyofaunal composition of our *P. erythrogaster* sites is similar to other reports in the literature, although the relative abundance of *Campostoma anomalum*, *Semotilus atromaculatus*, *Pimephales notatus* and *Phoxinus erythrogaster* varied. Assuming that habitat is a factor in determining the occurrence of *P. erythrogaster*, one could surmise that sites similar in ichthyofaunal composition, especially those with *P. erythrogaster* present, should likewise have similar habitat. Based on our study, the congruence between matrices of habitat similarity and ichthyofaunal composition supports this notion, thereby stressing the importance of habitat in explaining the local occurrence of *P. erythrogaster*. However, our measured environmental variables only explained 53% of the variance in *P. erythrogaster* occurrence at the microhabitat scale. Considering the amount of unexplained variance in *P. erythrogaster* occurrence, a portion could be due to 'noise,' which is common in ecological data (Gauch, 1982), or additional unmeasured factors. Although there was significant congruence between habitat and ichthyofaunal similarity matrices, the correlation of similarity values between sites was weak; that is, the ability to predict sites similar in ichthyofaunal composition based on habitat similarity was low. The low correlation between habitat similarity and ichthyofaunal composition suggests that although habitat is important, additional factors may be responsible for the local occurrence of *P. erythrogaster*.

Biotic interactions such as predation and interspecific competition may serve to regulate and maintain the organization and structure of stream fish communities (overview in Heins and Matthews, 1987). We have shown that *Semotilus atromaculatus*, *Campostoma anomalum* and *Pimephales notatus* are often associated with *Phoxinus erythrogaster*, although relative abundances of these species varied among sites. Cashner *et al.* (1979) found that these three species represented 78% of the total abundance in Bliss Creek, while in Clark Creek (Wilkinson Co.) they comprised only 37% (Table 3). We found that 77% of the total abundance among the six *P. erythrogaster* sites was represented by the three species. In Wisconsin, 39% of the total abundance was attributed to the three species (Becker, 1983). In addition, we found that standardized abundance for *S. atromaculatus* was consistently high among all sites where *P. erythrogaster* were present, whereas standardized abundance for the remaining species varied from site to site. Although the presence of piscivorous *S. atromaculatus* may imply increased risk of predation on *P. erythrogaster* (Cerri, 1983; Fraser *et al.*, 1987), it does not appear to limit *P. erythrogaster* abundance, but rather may assist reproduction by offering more potential nest sites for *P. erythrogaster*. Species of *Phoxinus* are known to spawn over nests or mounds of *Semotilus*, *Campostoma* and *Nocomis* (Smith, 1908; Raney, 1947; Settles and Hoyt, 1978; Starnes and Starnes, 1981) and thus the presence of these species is important for successful reproduction. Sites with high standardized abundances of *C. anomalum* and *Pimephales notatus*, however, typically had low standardized abundance of *Phoxinus erythrogaster*. Sites where either *C. anomalum* and/or *Pimephales notatus* were absent or their standardized abundances low, were typically higher in *Phoxinus erythrogaster* standardized abundance. The site with the highest standardized abundance of *P. erythrogaster* (Site 22) had neither species present. Cashner *et al.* (1979) speculated that the low abundance of *P. erythrogaster* in Bliss Creek in comparison to Clark Creek may be linked to the differences in species composition between the two systems. They reasoned that the limited carrying capacity of such a small stream would potentially enhance competitive interactions among fishes of similar trophic guilds (*C. anomalum*, *Pimephales notatus* and *Phoxinus erythrogaster*). However, without additional studies involving niche overlap and resource availability among these species, the role of biotic interactions as a causal factor in explaining *P. erythrogaster* occurrence is speculative.

Disturbance, either due to erosion or increased urban development, altered habitat quality among our study sites. That *Phoxinus erythrogaster* were not collected at two historic localities (Slack *et al.*, 1995), further suggests that their occurrence is influenced by declining habitat quality. One locality, Site 18, showed little habitat similarity to the remaining *P. erythrogaster* sites. This historic record is based on one individual collected in 1952 (UAIC 249.02) and represents the only record of *P. erythrogaster* within Hatcher Bayou. Since that time, this area has undergone extensive urbanization as the city of Vicksburg has expanded. The impact of urbanization along with the construction of a school within 200 m of the stream has likely altered instream habitat. As a consequence, episodic, low-intensity disturbances that are typically associated with urbanization (McDonnell and Pickett, 1990) may have been enough to extirpate the species (Weaver and Garman, 1994). In contrast, the other historic locality (Site 10) (USNM 2000048), along with a number of other sites (5, 7 and 9), were similar in habitat to the remaining sites where *P. erythrogaster* were present. However, Site 10 showed little ichthyofaunal similarity with sites where *P. erythrogaster* were present. We lack adequate information to comment on the historic ichthyofaunal composition at Site 10 and are uncertain whether habitat today is representative of past conditions.

An additional factor to consider is the role of historical events in determining community structure and organization of the Mississippi populations of *Phoxinus erythrogaster*. Mississippi and the remaining southeastern region have experienced a dynamic geologic past which has contributed to the formation of unique faunas and a high degree of endemism (Hocutt and Wiley, 1986; Wiley and Mayden, 1985). As the result of numerous glacial and interglacial periods, this area has been subjected to major sea level fluctuations which caused changes in drainage patterns and promoted periods of dispersal for stream fishes. Each event brought with it changes to the ichthyofaunal community (additions, losses) such that present-day ichthyofaunal composition is the sum of ichthyofaunal contributions resulting from all past geologic events. As a consequence, observed ecological interactions among species may be solely of historic origin or the result of contemporary forces (Mayden, 1987). We fully agree with this view and support the contention that historical influences should be considered when interpreting ecological patterns. We believe that the influence of historical constraints may provide a viable explanation for the observed pattern of occurrence of *P. erythrogaster* in Mississippi. However, we do not have data, nor was it the intent of this paper, to discern the relative influence of these factors on the occurrence of *P. erythrogaster*. The alternatives, biotic interaction and declining habitat quality, provide equally plausible explanations, but neither provides unequivocal evidence to support either claim.

Habitat and ichthyofaunal composition of western Mississippi stream fish assemblages containing *Phoxinus erythrogaster* are similar to those reported for other geographic areas. Because the presence of *P. erythrogaster* is strongly linked to specific habitat features, future conservation and management decisions should be directed to protect and ensure the quality of this habitat. Depicted patterns in *P. erythrogaster* occurrence and abundance may be related to declining habitat quality and/or increased biotic interaction. These scenarios provide a platform to pose testable hypotheses relating to community organization and structure among these populations within the framework of regional processes. Determining the origin of assumed biotic interactions (contemporary or historic) and examining their role in determining the occurrence of *P. erythrogaster* would allow one to further address specific questions regarding the importance of habitat to *P. erythrogaster*.

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