

LIFE HISTORY OF THE YAZOO DARTER (PERCIDAE: *ETHEOSTOMA RANEYI*),
A SPECIES ENDEMIC TO NORTH-CENTRAL MISSISSIPPI

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ABSTRACT

The Yazoo darter, *Etheostoma mneyi*, is restricted to tributaries of the Little Tallahatchie and Yocona Rivers (Yazoo River drainage) in north-central Mississippi. The species inhabits small, clear streams, many of which are spring-fed, and have a variety of substrate types including silt, clay, sand and gravel. In Morris Creek, a second-order stream in Lafayette County, Mississippi, *E. raneyi* was found in a diversity of microhabitats. *Etheostoma raneyi* is short-lived, with very few individuals living more than two years. Yazoo darters are sexually dimorphic, with males larger and more brightly colored than females. Both sexes become reproductively mature during the first year of life. The sex ratio of the Morris Creek population is female-biased. Like other members of subgenus *Nunostoma*, Yazoo darters use the egg-attaching spawning strategy. Batch fecundity of Yazoo darters is 52, and the average diameter of ova in this size class is 1.05 mm. Based on gonadal condition, the spawning season lasts from March to June. Yazoo darters are the most abundant fish in Morris Creek.

INTRODUCTION

Etheostoma mneyi is one of eight species of subgenus *Nanostoma* (snubnose darters) described since 1991, bringing the number of described species to 20. Additional species await scientific description. Snubnose darters are relatively short-lived, small, sexually dichromatic fishes that use the egg-attaching spawning strategy (Page, 1983). Most species inhabit flowing pools and riffles of small streams (Suttkus and Etnier, 1991). At least three species of subgenus *Nanostoma* are considered imperiled (Williams et al., 1989), due in part to their limited distributions. The restricted range and lack of life-history information for many species of subgenus *Nunostoma* have concerned conservationists. The objective of this study is to provide life history information necessary for protection of the Yazoo darter and to compare with life histories of other species of *Nanostoma*.

Most snubnose darters occur in southern tributaries to the Ohio River, Gulf Coastal drainages east of the Mississippi River, and lower Mississippi tributaries (Suttkus and Etnier, 1991). Many are endemic to single drainages or have limited geographical distributions (Boschung et al., 1992). The Yazoo darter (*Etheostoma mneyi* Suttkus and Bart) is endemic to small streams of the upper Yazoo River drainage, Mississippi (Figure 1). Suttkus et al. (1994) reported the species from 15 sites (five in the Yocona River and ten in the Little Tallahatchie), while

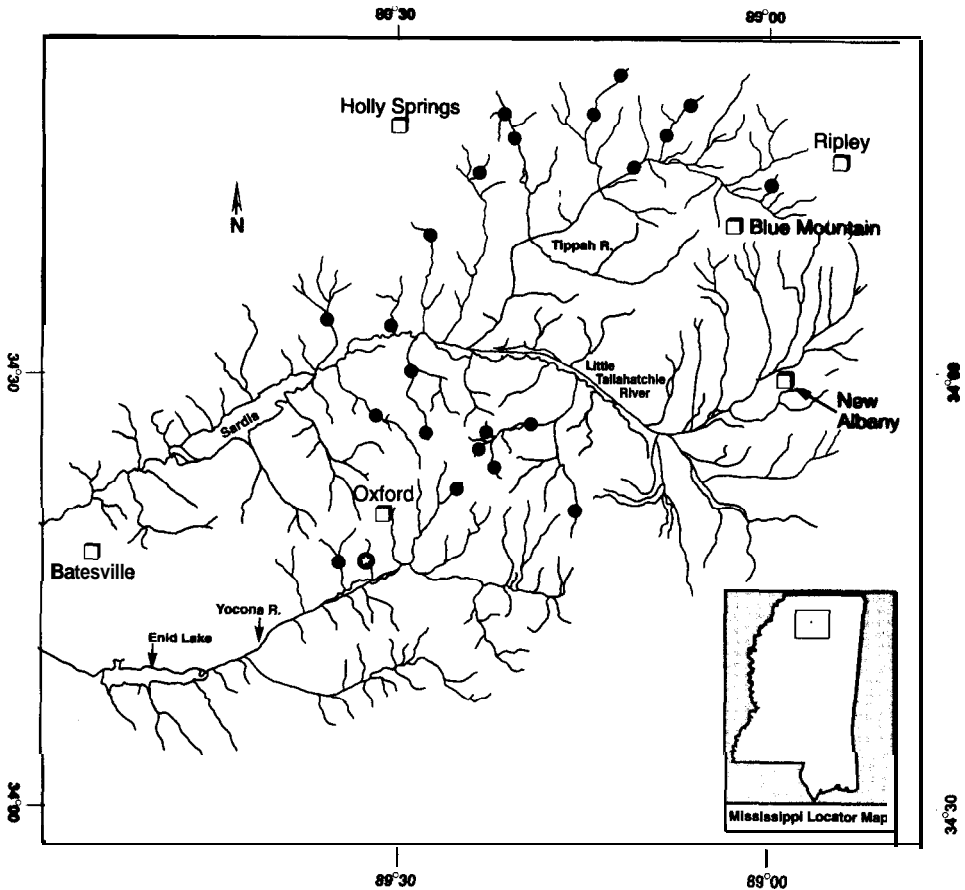


Figure 1. Distribution of *Etheostoma raneyi*. Study site is indicated by a star (modified from Thompson and Muncy, 1985).

in an unpublished status report Thompson and Muncy (1985) reported the Yazoo darter from 23 sites. Six sites listed by Suttkus et al. (1994) were not cited by Thompson and Muncy (1985), suggesting that the species may be found present at 29 sites.

STUDY SITE

Morris Creek is a clear, second-order stream that drains forested and agricultural lands for approximately 6.5 km before draining into the Yocona River. The study area is 3.2 km northeast of Taylor, Mississippi (T9S, R3W, sec. 16, 19 and 20) (Figure 1). At the study site the stream averages 3 m in width and has pool, riffle, and run habitats, and abundant woody debris. Substrates include clay, silty sand, coarse sand, gravel, and cobble. A narrow riparian zone is present, but much of the surrounding land is used for row crops or pasture. Yazoo darters used for spawning observations were collected from two streams: Lee Creek and an unnamed tributary to Bay Springs Branch, both of the Little Tallahatchie drainage, Lafayette County, Mississippi. The tributary to Bay Springs Branch is

within the University of Mississippi Biological Field Station (T7S,R2W, sec. 34); its average width is approximately 1.5 m, and the dominant substrate is sand. Woody debris and submerged aquatic vegetation (primarily *Sparganium*) are common. Lee Creek (T7S,R3W, sec. 1) averages 3 m in width and substrates include clay, silty sand, coarse sand, gravel, and cobble. Woody debris is common, and much of the surrounding land is forested.

MATERIALS AND METHODS

Yazoo darters were collected monthly from March 1993 to May 1994; two samples per month were made March-May 1994. All sampling was done using a three-meter-long minnow seine, and an effort was made to sample a wide variety of microhabitats. A general description of habitat type (run, riffle, pool, or undercut bank) was made for all seine hauls. At every location where a Yazoo darter was collected, the following habitat variables were measured: water depth and velocity (average of three measurements of each), substrate composition (percent composition by particle size, estimated by the modified Wentworth scale outlined in Ross et al., 1990), stream width, percent canopy cover, and the percent and make-up of instream cover. The identity and abundance of other species of fishes collected was recorded for all seine hauls. Exceptions are for species of *Fundulus* and *Erimyzon* that were not identified to species in the field. For the purpose of Table 1, species of *Lepomis* and *Micropterus* were lumped. Specimens of Yazoo darters were preserved in 5% buffered formalin; other fishes were released.

Homogeneity of distribution of darters among the five habitat types was evaluated using $R \times C$ G-tests of independence (Sokal and Rohlf, 1981). The relationship between darter density and habitat type was further explored using principal components analysis (PCA) with Varimax rotation, using the SYSTAT software package (Wilkinson, 1990). A scree test indicated the number of meaningful components. Standardized factor scores for all combinations of components were plotted and numbers of darters were overlaid on the factor score plots. This two-step procedure does not assume linearity between abundance of fishes and environmental variables and is appropriate for these data (Ross et al., 1987; Ross et al., 1990).

Sex, standard length (SL), and age of preserved darters were determined in the laboratory. Standard length was measured to the nearest 0.1 mm using dial calipers. Age was determined to the nearest month by counting scale annuli. April was used as month zero, since it is near the middle of the spawning season. Scales for age analysis were removed above the lateral line and near the tip of the depressed pectoral fin.

Seasonal changes in gonad mass for both sexes were quantified using gonadosomatic index (GSI). Gonads and eviscerated specimens were dried at 55°C for 24 hours and weighed to the nearest 0.001 gm. Gonadosomatic index was calculated by dividing gonad mass by adjusted somatic mass (mass of eviscerated specimen) and multiplying by 1000. The reproductive condition of males was classified as latent or mature by examination of testes. Latent testes were tiny strands of clear tissue; mature testes were enlarged and opaque. The reproductive condition of females was determined by examination of ovaries and their classification into one of six developmental stages according to Heins and Baker (1993): latent (LA), early maturing (EM), late maturing (LM), mature (MA), ripening (MR), or ripe (RE). Five ova were counted and measured in each of the

TABLE 1. Relative abundance of occurrence of fishes in Morris Creek, Lafayette County, Mississippi, 1993-1994 (n=12 samples). Fishes were identified in the field and released; fishes in the genera *Lepomis*, *Micropterus*, *Fundulus* and *Erimyzon* are lumped for the purpose of this table (see text for explanation).

<i>Etheostoma raneyi</i>	.207	<i>Semotilus atromaculatus</i>	.036
<i>Cyprinella camura</i>	.168	<i>Erimyzon</i> spp.	.021
<i>Percina sciera</i>	.102	<i>Etheostoma whipplei</i>	.018
<i>Fundulus</i> spp.	.168	<i>Micropterus</i> spp.	.012
<i>Noturus phaeus</i>	.079	<i>Hypentelium nigricans</i>	.010
<i>Pimephales notatus</i>	.073	<i>Etheostoma proeliare</i>	.010
<i>Notropis rafinesquei</i>	.057	<i>Etheostoma parvipinne</i>	.003
<i>Etheostoma lynceum</i>	.040	<i>Etheostoma nigrum</i>	.002
<i>Lepomis</i> spp.	.040	<i>Pimephales vigilax</i>	.001
		<i>Etheostoma swaini</i>	<.001

three largest size classes for 43 females from seven samples taken during the breeding season (March-June 1993; March-May 1994). These size classes were distinct, and separated by at least 0.30 mm of diameter. The diameter of each ovum was expressed as an average of the smallest and largest diameters to account for irregularity in shape (as typical for many darter species, the eggs were concave in shape). Measurements were made using a dissecting microscope and ocular micrometer. Reproductive data were analyzed using the SYSTAT software package (Wilkinson, 1990).

Spawning mode was determined by observation of breeding activities in aquaria. Reproductively active males (identified by bright spawning coloration) and females (identified by distended abdomens containing ripe eggs) were collected from a tributary to Bay Springs Branch (1993 and 1994) and Lee Creek (1995) and transported to the laboratory. Animals were placed in 84 or 840 liter aquaria and maintained at 19-21°C. Aquaria contained the following substrates known to be used for spawning by other darter species: logs, plants and boulders (used by egg-attachers); gravel and sand substrate (used by egg-buriers); and cavities (used by egg-clumpers and egg-clusterers) (Page, 1985). Study animals were collected on 17 April 1993 (6 females, 3 males), 10 March 1994 (5 females, 4 males), and 25 March 1995 (2 females, 2 males); spawning usually occurred within two days of capture. Observations were made several times a day for 10 days following introduction into the aquaria. Observation periods were from 15 minutes to 2 hours. Spawning events were recorded with an 8 mm video camera. A total of seven spawning pairs were observed. The spawning description is based on the observations and from reviewing video tapes of spawning episodes. Five eggs from each spawning event were measured to the nearest 0.01 mm with a dissecting microscope and ocular micrometer.

RESULTS

Etheostoma raneyi was the most abundant fish in Morris Creek (Table 1). Other common fishes included bluntface shiner (*Cyprinella camura*), dusky darter (*Percina sciera*), topminnows (*Fundulus notatus* and *Fundulus olivaceus*), brown madtom (*Noturus phaeus*), and bluntnose minnow (*Pimephales notatus*). Other species of *Etheostoma* present in the stream included redfin darter (*Etheostoma whipplei*), cypress darter (*Etheostoma proeliare*), goldstripe darter (*Etheostoma parvipinne*), johnny darter (*Etheostoma nigrum*), brighteye darter (*Etheostoma lynceum*), and gulf darter (*Etheostoma swaini*) (Table 1).

TABLE 2. occurrence of Yazoo darters (*Etheostoma raneyi*) among five habitat types in Morris Creek, Lafayette County, Mississippi. Data were pooled from 10 sample dates, 1993-1994.

HABITAT	NUMBER OF SAMPLES	NUMBER OF DARTERS	PERCENT WITH DARTERS
Run	52	23	44%
Swift riffle	74	30	41%
Moderate riffle	105	46	44%
Undercut bank	100	47	47%
Pool	55	37	67%

HABITAT. *Etheostoma raneyi* was a habitat generalist. Yazoo darters were evenly distributed among runs, swift riffles, moderate riffles, and undercut banks, but were slightly more common in pools (Table 2). Overall comparison of all five habitat types showed a significant association between habitat and darter occurrence ($G=11.00, p<0.03, 4 \text{ df}$). However, when pools were dropped from the analysis, the result became nonsignificant ($G=0.73, p<0.87, 3 \text{ df}$). Principal components analysis of habitats associated with darter occurrence showed that darters were found in a wide range of habitat configurations (Figure 2). Similar overlays of darter density were made for all other combinations of factor plots, but no relationships were demonstrated. Three components explained 64% of the total variance (Table 3). Principal component I (factor I) ordinated darter occurrences along a gradient from deep sites with fine substrates and low velocity to shallow sites with coarse substrates and high velocity. Principal component II (factor II) ordinated occurrences along a gradient of sites with low instream cover and a high percentage of canopy cover to sites with high instream cover and a low percentage of canopy cover, while component III described an inverse relationship between stream width and water velocity.

DEMOGRAPHICS. Age and sex composition of the *E. raneyi* population in Morris Creek is shown in Table 4. Sex ratios were significantly female-biased in the age one class, and for the total sample. The oldest female was 45.5 mm SL and 34 months of age; the oldest male was 52.6 mm SL and 33 months of age. Mean length of males was longer (SL) (36.4 mm, $SD=6.1$) than females (34.5, $SD=5.2$) ($t=3.3; p<0.001$) in the total sample.

GROWTH. Growth of *E. raneyi* was rapid during the first months of life, declined between four and ten months of age, and leveled off after ten months (Figure 3). Standard length (mm) was positively correlated with age (months) for 129 males ($SL=19.484+18.388*\log X, r=0.7, p<0.01$) and 199 females ($SL=17.346+17.366*\log X, r=0.8, p<0.01$). By seven to nine months of age, mean length of males was greater than that of females (samples were lumped for these three months due to sample size) ($t=6.5, p<0.001$; mean SL males=39.46 mm, $n=19$; females=33.01 mm, $n=17$), suggesting that males grow faster than females do.

GONADAL DEVELOPMENT. All females >30 mm SL (8 months of age and older) and all males >34 mm SL (8 months of age and older) were reproductively mature in March of 1993 and 1994. Males developed intense breeding coloration (described by Suttkus et al., 1994) and mature testes in December (Figure 4). Some males had mature testes throughout the spring and early summer, but the testes of all males were latent by July. This prolonged period of reproductive readiness is supported by the gonadosomatic index (GSI) for males, which

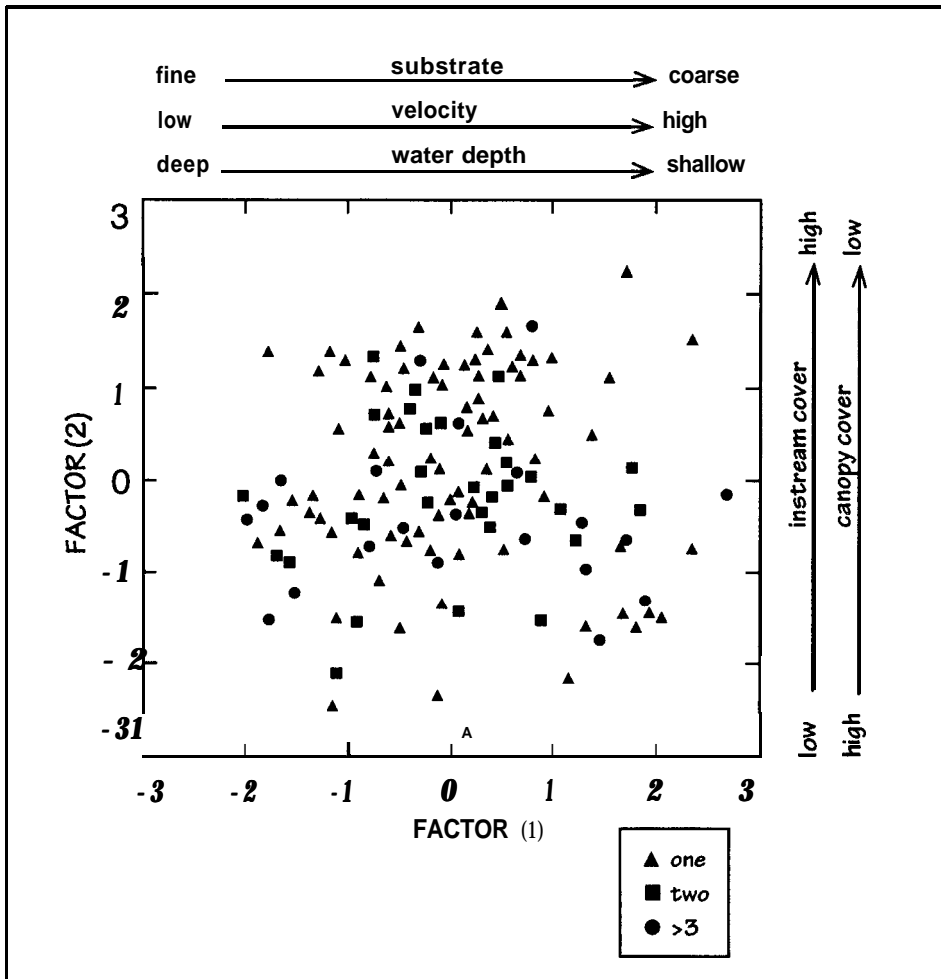


Figure 2. Overlay of numbers of *Etheostoma raneyi* samples on plot of standardized factor scores for Factor 1 and Factor 2.

increases during late winter, peaks in early spring, and declines in the summer (Figure 5).

Ovaries of females begin maturation in late fall, and some individuals have ripe ovaries by early spring (Figure 6). All ovaries are latent by July, similar to the pattern seen in males. The GSI for females also closely follows the pattern of development in males (Figure 5); the values of GSI are much higher in females than in males, illustrating the higher investment by females in ova.

Standard length was positively correlated with the GSI of males ($r^2=0.183, p<0.006$; $GSI=5.455+3.074$ SL) and of females ($r^2=0.127, p<0.002$; $GSI=-1.351+0.238$ SL) (Figure 7). There was also a relationship between SL and somatic weight for females ($r^2=0.942, p<0.001$; $somatic\ weight=-0.441+0.017$ SL),

TABLE 3. Variable loadings > 0.4 (loading value of 0.398 was retained) on three principal component axes, after varimax rotation. Percent variance explained by each component is given in parentheses.

VARIABLE	PRINCIPAL COMPONENT		
	I (26.0%)	II (19.0%)	III (18.5%)
Substrate	0.727		
Velocity	0.698		0.398
Depth	-0.665		
Cover		0.773	
Canopy		-0.694	
Width			-0.933

and for males ($r^2=0.942, p<0.001$; somatic weight= $-0.666+0.023$ SL) and males and females had virtually identical relationships between these variables (Figure 8).

By June, the number of ova in all size classes decreases (Figure 9). Peak numbers were seen in early spring, corresponding to peak GSI values and percentages of ripe ovarian stages. The mean number and diameter of ova in the three largest size classes for 43 females sampled during the breeding season are, from largest to smallest: 52 (SD=20), 1.05 mm (SD=0.11); 80 (SD=35), 0.74 mm (SD=1.10); 303 (SD=129), 0.38 mm (SD=0.03). Both the number and diameter of ova increased with standard length ($r^2=0.480, p<0.001$; number= $64.732+3.243$ SL; $r^2=0.376, p<0.001$; diameter= $0.524+0.014$ SL) (Figure 10).

SPAWNING BEHAVIOR. Male Yazoo darters are nonterritorial, but display aggression toward conspecific males when a male engaged in courtship or spawning is approached by another male. Males react by chasing the intruder, or performing stationary lateral displays with erect fins. No elaborate courtship displays were observed in this species. Prior to spawning, males typically pursue females as they move about the substrate selecting a spawning site. When a female is receptive, the male mounts her back with his caudal peduncle to her side. The pair then vibrate as the female attaches an egg to the spawning substrate. Eggs are usually attached singly to the substrate. Of the 29 episodes observed, 18 (62%) eggs were attached to a submerged log, 6 (21%) to plants or plant roots, 3 (10%) to the gravel substrate, and 2 (7%) to large rocks. The average diameter of five eggs removed from an aquarium was 1.28 mm. Typically, a single pair spawned numerous times in succession, but not all mountings

TABLE 4. Age and sex composition of Yazoo darters from Morris Creek, Lafayette County, Mississippi, 1992-1993.

	AGE GROUP				
	0	1+	2+	3+	TOTAL
Male	71	49	8	1	129
Female	82	106	11	0	199
Total	153	155	19	1	328
χ^2	0.79, $p=0.3$	20.90, $p<0.001$	0.47, $p=0.49$		14.94, $p<0.001$
Sex ratio (female:male)	1.2:1	2.2:1	1.4:1		1.5:1

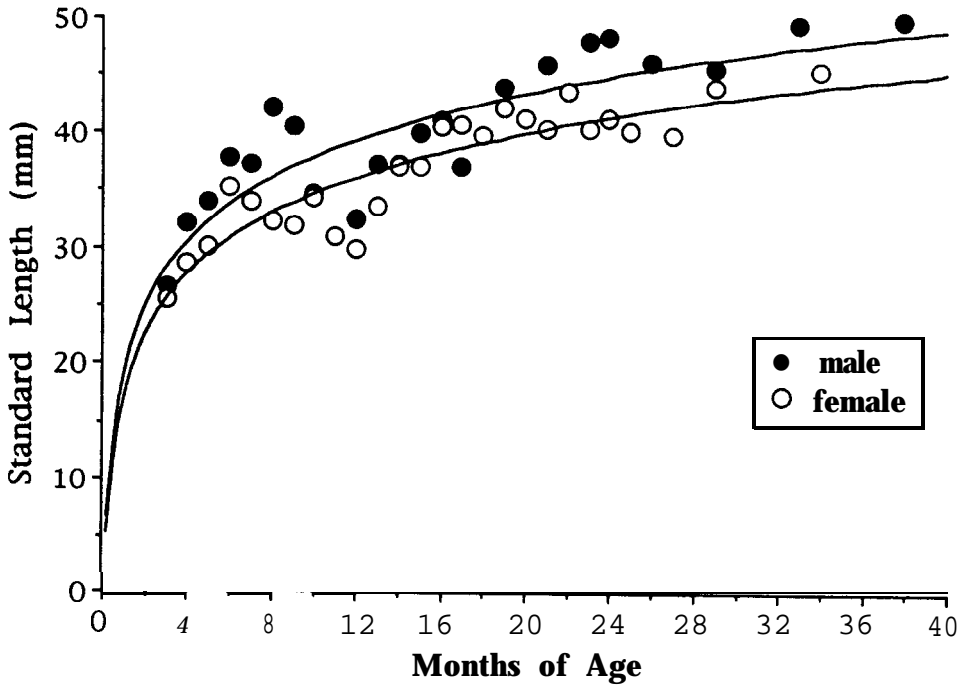


Figure 3. Growth curves for males and females of *Etheostoma raneyi*. Points represent sample means.

resulted in the release of an egg. Males and females were promiscuous, and no parental care was provided to the eggs.

DISCUSSION

The Yazoo darter (*Etheostoma raneyi*) is one of 20 described species of snub-nose darters, subgenus *Nanostoma* (Page, 1981). Typical habitat of most adults of subgenus *Nanostoma* was described by Page and Mayden (1981) as clean pools with moderate current and bedrock, cobble or gravel substrate. Exceptions among upland *Nanostoma* species are *Etheostoma etnieri*, which prefers riffles and runs (Bouchard, 1977), *Etheostoma zonale*, which inhabits rocky, vegetated riffles (Page and Mayden, 1981), and *Etheostoma coosae*, which occurs in all stream mesohabitats (riffles, runs, pools) over gravel or cobble substrate (O'Neil, 1981). Habitat descriptions of *Nanostoma* species found in lowland streams reflect the physical characteristics of these streams, which usually have sand and gravel substrates and low to moderate gradients. *Etheostoma zonistium*, a lowland species, occurs predominantly in stream margin habitat with sand or sand and gravel substrate, and is found less frequently in run and riffle habitat (Carney and Burr, 1989). *Etheostoma pyrrhogaster* is found in stream margin, pool, run and riffle habitat over sand substrate (Carney and Burr, 1989). *Etheostoma raneyi* is also found in lowland streams, and like *E. coosae* (O'Neil, 1981) and *E. pyrrhogaster*, is found in all habitats. Our analysis showed that *E. raneyi* individuals were evenly distributed among runs, swift riffles, moderate riffles and undercut banks, but were slightly more common in pools. However, higher darter density

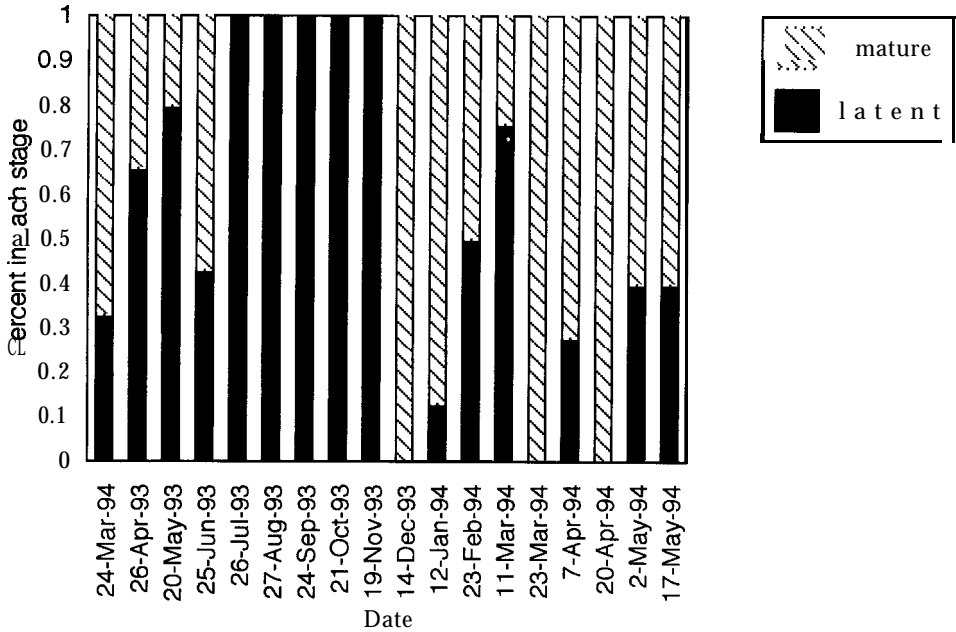


Figure 4. Monthly changes in testicular development of *Etheostoma raneyi* males

in any particular habitat was not demonstrated by the overlay of darter density on plots of PCA factor scores. *Etheostoma raneyi* was the most common species in Morris Creek, and was found in most seine samples that had fishes. Similarly, Carney and Burr (1989) found that *E. zonistium* was the most common species found in West Fork Clarks River, Kentucky.

Like other species in the snubnose group, Yazoo darters are short-lived, with very few individuals surviving more than two years (33-34 months). Some individuals of *E. zonistium*, *E. pyrrhogaster* and *E. coosae* live more than two years (Carney and Burr, 1989; O’Neil,1981), while the maximum life span of *E. simoterum* is just 18 months (Page and Mayden, 1981). The longest life span reported for a *Nanostoma* species is for *E. zonale*, with individuals that survive more than three years (Lachner et al., 1950).

The sex ratio of *E. raneyi* is female-biased for age group one, and for the total sample. Female bias has been reported for components of populations of *E. coosae*(O’Neil,1981), *E. simoterum* (Page and Mayden,1981), and *E. zonistium* (Carney and Burr, 1989), and may be caused by differential mortality in the brightly colored males (Carney and Burr, 1989).

As reflected by higher GSI, female *E. runeyi* invest more than males do in gonadal tissue. This is typical of most fishes (Moyle and Cech,1988), and suggests that females invest more in reproduction. However, male investment in reproduction could be manifested not only in gonadal tissue, but in sexually selected traits as well. In many species, larger males have a reproductive advantage over smaller males, due to intrasexual competition for females or female choice for larger males. This size difference could be manifested in greater length (SL) of males or in greater somatic weight. In *E. runeyi*, males do not invest more than females in somatic weight, but achieve longer lengths (SL), as

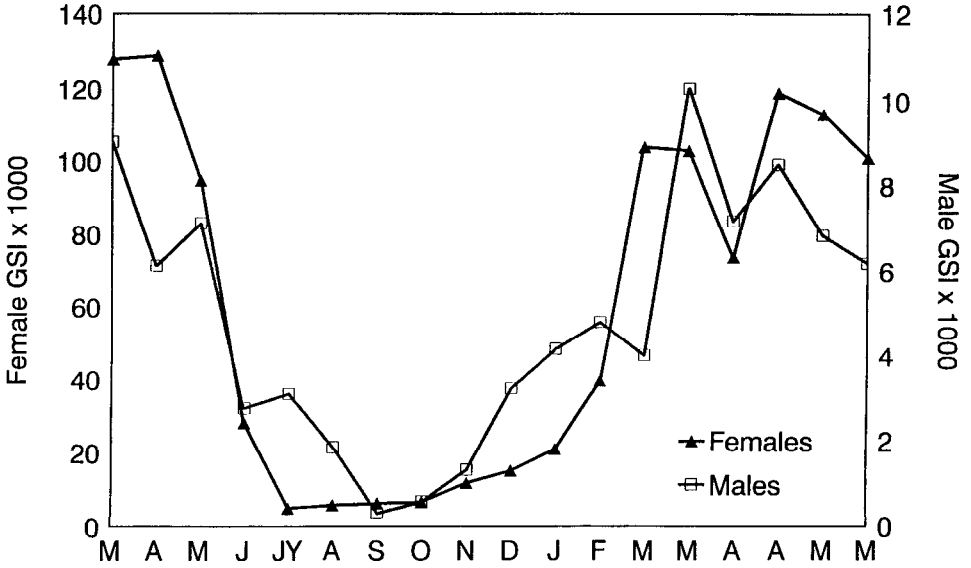


Figure 5. Monthly changes in mean gonadosomatic index of *Etheostoma raneyi* males and females.

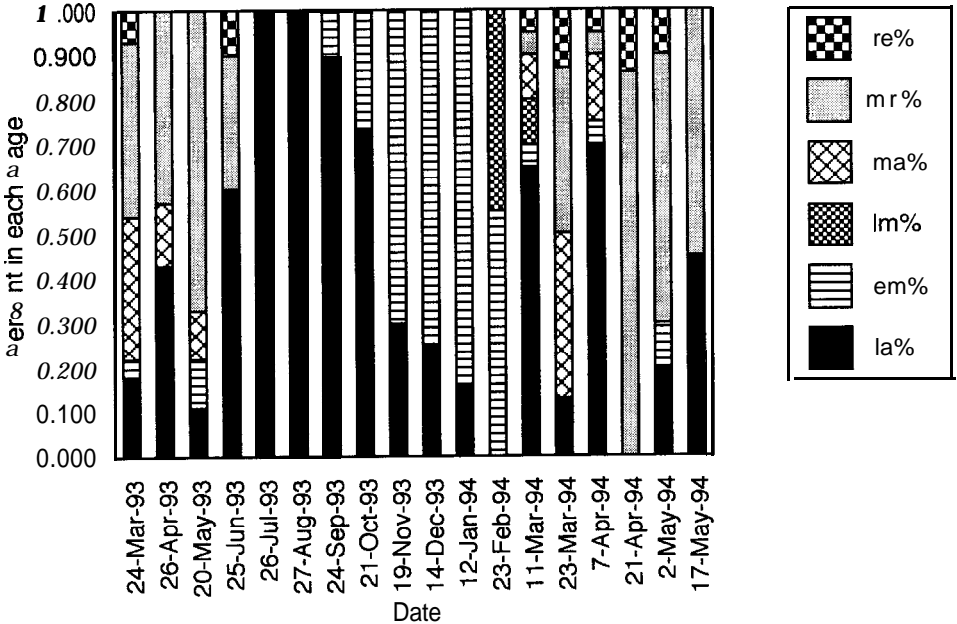


Figure 6. Monthly changes in ovarian development of *Etheostoma raneyi* females. Ovarian stages are latent (la), early maturing (em), late maturing (lm), mature (ma), and ripe (re).

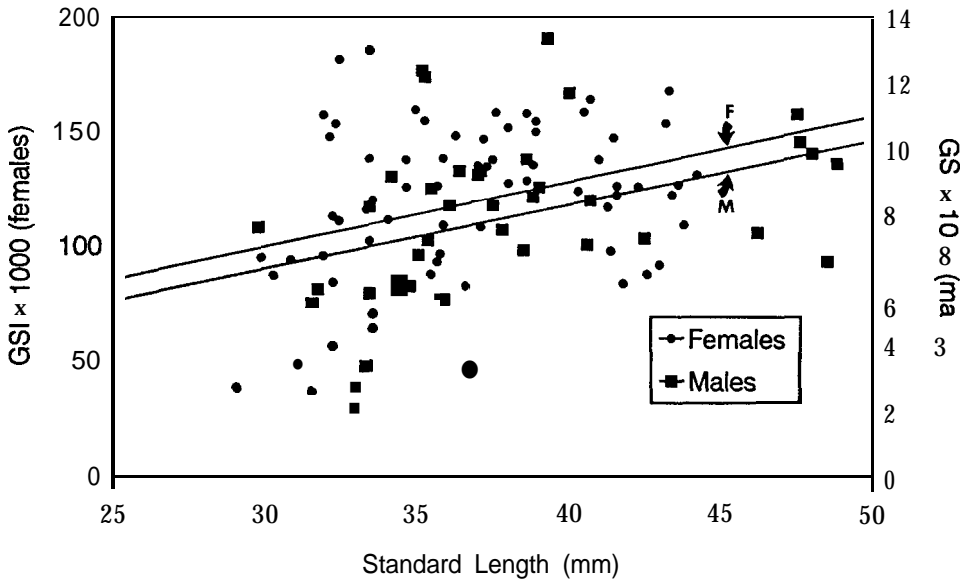


Figure 7. Relationship between standard length (SL) and gonadosomatic index (GSI) for *Etheostoma raneyi* males and females.

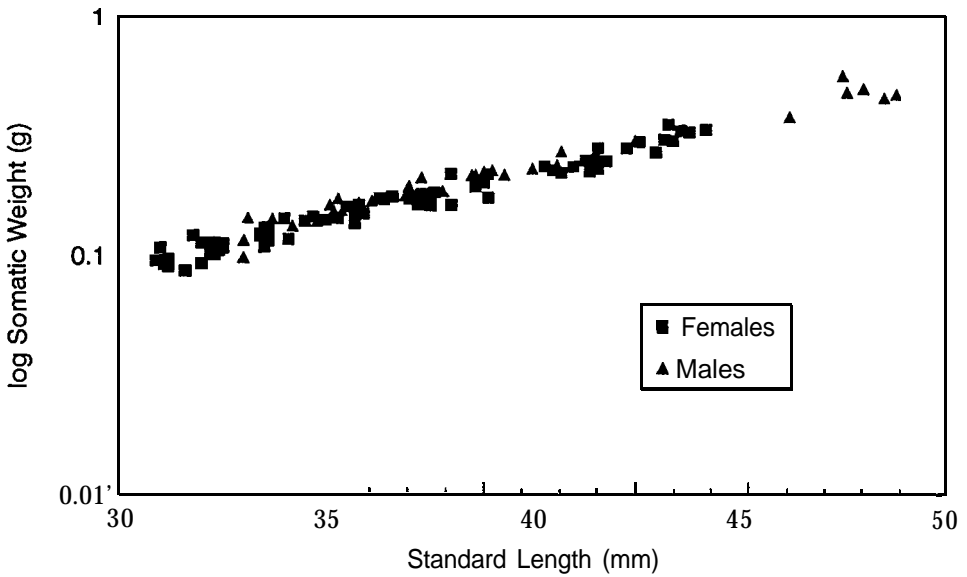


Figure 8. Relationship between standard length (SL) and somatic weight for *Etheostoma raneyi* males and females.

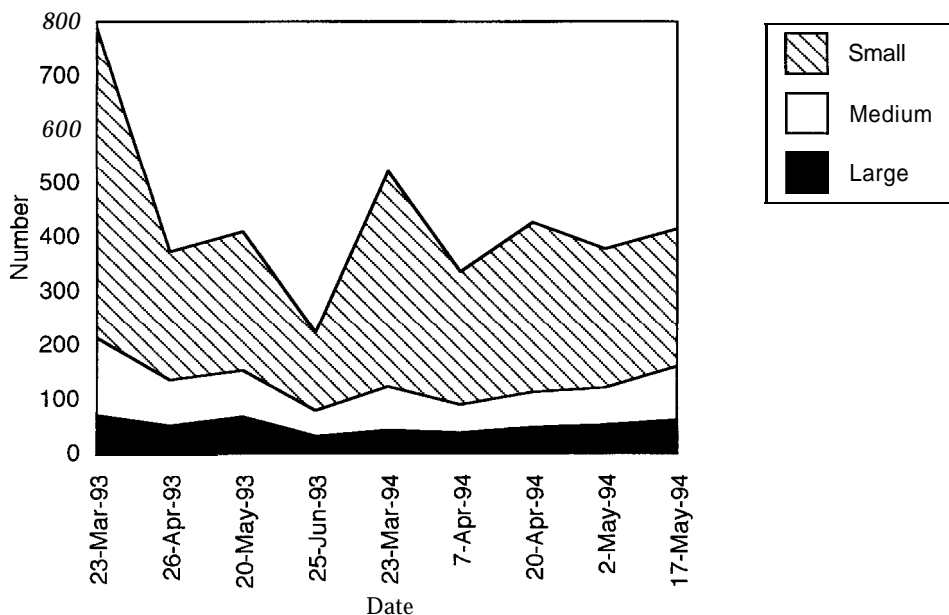


Figure 9. Changes in the number of ova in the three largest size classes of *Etheostoma raneyi* females during the 1993 and 1994 breeding seasons.

in other *Nanostoma* species (Page and Mayden, 1981; Carney and Burr, 1989). If males expend more energy than females do on courtship and aggression during the breeding season, males would be predicted to lose more somatic weight during that time. This is not suggested by our data, but our samples were lumped over the duration of the breeding season, and may not reveal such subtle relationships. Males also invest in bright breeding colors that are undoubtedly the result of sexual selection, although this has yet to be tested for darters. Bright colors may be responsible for differential mortality in males due to predation, and this could also be viewed as a cost of reproduction. More research on reproductive investment in darters is needed before an apparent differential investment by the sexes is understood.

The spawning period for *E. mneyi* is from March through June. A relatively long spawning season is also found in *E. pyrrhogaster* and *E. zonistium* (Carney and Burr, 1989), and in *E. rafinesquei* (Weddle and Burr, 1991). April has been reported as the peak spawning season for *E. barrenense* and *E. rafinesquei* (Stiles, 1974; Page and Burr, 1982), *E. coosae* (O'Neil, 1981), and *E. simotolum* (Page and Mayden, 1981).

Comparing the fecundity and diameter of ova for fishes is difficult, due to differences in methodology among studies. The mean number of ova in the largest size class, or batch fecundity, of female *E. raneyi* was 52 ($n=43$ females), and the mean diameter of these ova was 1.05 mm. The mean batch fecundity of *E. rafinesquei* is 48.3 (Weddle and Burr, 1991).

Etheostoma raneyi shares the egg-attaching spawning strategy with all other species of *Nanostoma* for which spawning behavior is known (Page, 1985; Keevin et al., 1989). These species exhibit no parental care, and deposit eggs in small

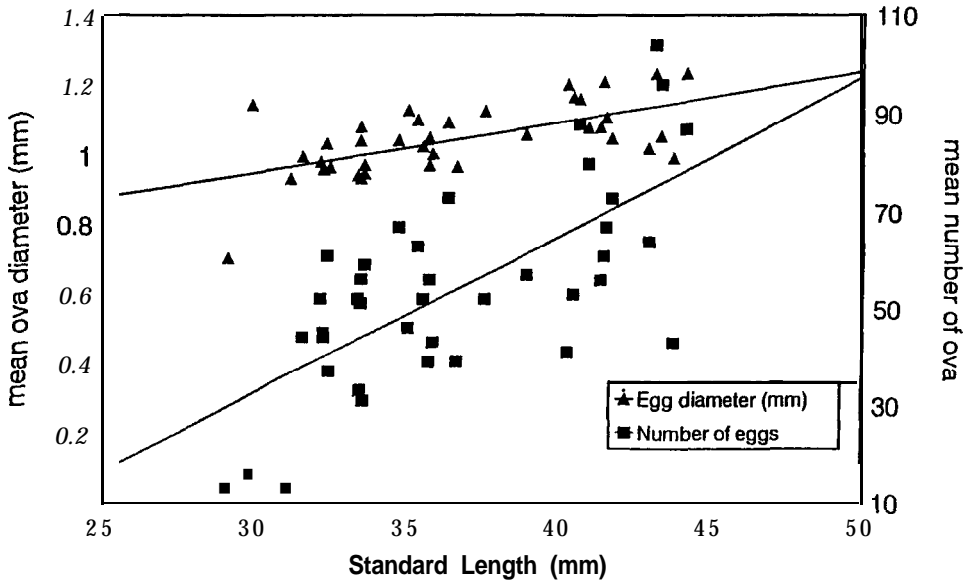


Figure 10. Relationship between number and diameter of ova and standard length (SL) of *Etheostoma raneyi* females.

numbers. Male *E. raneyi* did not maintain territories associated with particular spawning substrates, but were aggressive to other males. Such moving territories were also observed in *E. barrenense* and *E. rafinesquei* (Stiles, 1974), *E. simoterum* (Page and Mayden, 1981), *E. flavum* (Keevin et al., 1989), and apparently *E. pyrrhogaster* and *E. zonistium* (Carney and Burr, 1989). Page (1983) proposed that the egg-attaching strategy provided some protection from egg predation. This tendency to place the eggs in several places probably precludes economic defensibility of any given spawning substrate and, as a result, territoriality is not seen in these species.

Although *E. raneyi* has a limited distribution, within its range it can be the most common species, and does not appear to be in danger of extinction. However, individual populations of *E. raneyi* should be carefully monitored, because the small streams that are typical habitat for the species are often targeted for habitat alteration, or are degraded by poor land use. For a species with a limited distribution, the loss of several populations and resulting fragmentation of the species' range could quickly lead to imperilment. With *E. raneyi*, monitoring and habitat protection could alleviate retroactive recovery efforts currently needed for other species of subgenus *Nanostomn*.

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LITERATURE CITED

- BOSCHUNG, H. T., R. L. MAYDEN, AND J. R. TOMELLERI. 1992. *Etheostoma chermocki*, a new species of darter (Teleostei: Percidae) from the Black Warrior River drainage of Alabama. *Bull. Alabama Mus. Nat. Hist.* 13: 11-20.
- BOUCHARD, R. W. 1977. *Etheostoma etnieri*, a new percid fish from the Caney Fork (Cumberland) River system, Tennessee, with a redescription of the subgenus *Ulocentra*. *Tulane Stud. Zool. Bot.* 19: 105-130.
- CARNEY, D. A. AND B. M. BURR. 1989. Life histories of the bandfin darter, *Etheostoma zonistium*, and the firebelly darter, *Etheostoma pyrrhogaster*, in Western Kentucky. *Illinois Nat. Hist. Surv. Biol. Notes* 134 (16 pp.).
- HEINS, D. C. AND J. A. BAKER. 1993. Reproductive biology of the brighteye darter, *Etheostoma lynceum* (Teleostei: Percidae), from the Homochitto River, Mississippi. *Ichthyol. Explor. Freshwaters* 4: 11-20.
- KEEVIN, T. M., L. M. PAGE, AND C. E. JOHNSTON. 1989. The spawning behavior of the saffron darter (*Etheostoma flavum*). *Trans. Kentucky Acad. Sci.* 50: 55-58.
- LACHNER, E. A., E. F. WESTLAKE, AND P. S. HANDWERK. 1950. Studies on the biology of some percid fishes from western Pennsylvania. *Amer. Midl. Nat.* 43: 92-111.
- MOYLE, P. B. AND J. J. CECCH. 1988. *Fishes: An Introduction to Ichthyology*. Prentice Hall, Englewood Cliffs, New Jersey (559 pp.).
- O'NEIL, P. E. 1981. Life history of *Etheostoma coosae* (Pisces: Percidae) in Barbaree Creek, Alabama. *Tulane Stud. Zool. Bot.* 23: 75-83.
- PAGE, L. M. 1981. The genera and subgenera of darters (Percidae, Etheostomatini). *Occas. Pap. Mus. Nat. Hist. Univ. Kansas* 90 (69 pp.).
- PAGE, L. M. 1983. *Handbook of Darters*. T.F.H. Publications, Inc., Neptune City, New Jersey (271 pp.).
- PAGE, L. M. 1985. Evolution of reproductive behaviors in percid fishes. *Illinois Nat. Hist. Surv. Bull.* 33: 275-295.
- PAGE, L. M. AND B. M. BURR. 1982. Three new species of darters (Percidae, *Etheostoma*) of the subgenus *Nanostoma* from Kentucky and Tennessee. *Occas. Pap. Mus. Nat. Hist. Univ. Kansas* 101 (20 pp.).
- PAGE, L. M. AND R. L. MAYDEN. 1981. The life history of the Tennessee snubnose darter, *Etheostoma simoterrum*, in Brush Creek, Tennessee. *Illinois Nat. Hist. Surv. Biol. Notes* 117 (11 pp.).
- ROSS, S. T., R. H. MCMICHAEL, JR., AND D. L. RUPLE. 1987. Seasonal and diel variation in the standing crop of fishes and macroinvertebrates from a Gulf of Mexico surf zone. *Estuarine Coastal Shelf Sci.* 25: 391-412.
- ROSS, S. T., J. G. KNIGHT, AND S. D. WILKINS. 1990. Longitudinal occurrence of the bayou darter (Percidae: *Etheostoma rubrum*) in Bayou Pierre—response to stream order or habitat availability? *Polish Arch. Hydrobiol.* 37: 221-233.
- SOKAL, R. R. AND F. J. ROHLF. 1981. *Biometry* (ed. 2). W. H. Freeman and Company, New York (859 pp.).
- STILES, R. A. 1974. The reproductive behavior of the Green and Barren River *Ulocentra* (Osteichthyes: Percidae: *Etheostoma*). *ASB Bull.* 21: 86-87.
- SUTTKUS, R. D. AND D. A. ETNIER. 1991. *Etheostoma tallapoosae* and *E. brevirostrum*, two new darters, subgenus *Ulocentra*, from the Alabama River drainage. *Tulane Stud. Zool. Bot.* 28: 1-24.
- SUTTKUS, R. D., R. M. BAILEY, AND H. L. BART. 1994. Three new species of *Etheostoma*, subgenus *Ulocentra*, from the Gulf Coastal Plain of southeastern United States. *Tulane Stud. Zool. Bot.* 29: 97-126.
- THOMPSON, K. W. AND R. J. MUNCY. Undated (submitted in 1985). A status report on the Yazoo River darter, *Etheostoma (Ulocentra)* sp. in northern Mississippi. U.S. Fish and Wildlife Service Report, Contract 14-16-009-1543.
- WEDDIE, G. K. AND B. M. BURR. 1991. Fecundity and the dynamics of multiple spawning in darters: an in-stream study of *Etheostoma rafinesquei*. *Copeia* 1991: 419-433.
- WILKINSON, L. 1990. *SYSTAT: The System for Statistics*. SYSTAT, Inc., Evanston, Illinois.
- WILLIAMS, J. E., J. E. JOHNSON, D. A. HENDRICKSON, S. CONTRERAS-BALDERAS, J. D. WILLIAMS, M. NAVARRO-MENDOZA, D. E. MCALLISTER, AND J. E. DEACON. 1989. Fishes of North America: endangered, threatened, or of special concern. 1989. *Fisheries* 14: 2-20.

