

## Life History of a Peripheral Population of Bluespotted Sunfish *Enneacanthus gloriosus* (Holbrook), with Comments on Geographic Variation

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**ABSTRACT.**—*Enneacanthus gloriosus* occurs in coastal plain drainages from New York to Florida and W to Mississippi, but little is known about its life history. *Enneacanthus gloriosus* is smaller and shorter-lived in Mississippi than in eastern populations. The spawning season of *E. gloriosus* ranges from April to September and gonadosomatic index values were highest between April and August, peaking in May with an additional but lower peak in August. Ripe eggs are also found during every month of the spawning season. These data indicate *E. gloriosus* is a multiple batch spawner. The sex ratio did not differ from 1:1, the diameter of mature ova averaged 0.68 mm, and the number of ripe ova per female averaged 117.2. *Enneacanthus gloriosus* at the periphery of its western distribution in Mississippi exhibit substantial variation in a number of life-history patterns including size, age, length at maturity and spawning season compared to populations ranging from New Jersey to Florida.

### INTRODUCTION

The natural range of the bluespotted sunfish, *Enneacanthus gloriosus* (Holbrook) is the Atlantic slope from southern New England to Florida (Loftus and Kushlan, 1987) extending westward to the Jourdan River, Mississippi (Peterson and Ross, 1987). *Enneacanthus gloriosus* is the most ubiquitous of the three *Enneacanthus* species throughout this range. It is the only *Enneacanthus* in Mississippi and inhabits backwaters of drainages characterized by submerged aquatic vegetation and soft muddy substrate (Breder and Redmond, 1929; Lee and Gilbert, 1980; Peterson and VanderKooy, 1997).

Body size of *Enneacanthus gloriosus* varies geographically with a maximum of 85 mm total length (TL) in the NE (Hildebrand and Schroeder, 1928; Breder and Redmond, 1929) to a maximum reported size from Georgia and Florida of 77 mm TL (McLane, 1955; Gunter and Hall, 1965; Hellier, 1967; Fox, 1969; Laerm and Freeman, 1986). Peterson and VanderKooy (1997) reported a maximum size of 58.4 mm TL (44.5 mm standard length (SL) in coastal Mississippi.

Spawning season and length at first reproduction of *Enneacanthus gloriosus* may also vary geographically. Breder and Redmond (1929) found the *E. gloriosus* breeding season extended from at least July through early September in New Jersey, and Anjard (1974) stated that spawning occurred in the Potomac River, Virginia, in May and June. In contrast, gravid female *E. gloriosus* were noted from April through October in Florida (McLane, 1955; Hellier, 1967; Fox, 1969). *Enneacanthus gloriosus* also matured at a larger size in northern latitudes. For example, Raney (1965) noted that *E. gloriosus* spawn at ~51 mm TL in New York, with the onset of gonadal development being 40 mm SL for males and 42 mm SL for females in New Jersey (Breder and Redmond, 1929). In contrast, Fox (1969) reported size at onset of gonadal development to be ~21.7 mm TL (~16.7 mm SL) for females in Florida.

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Peterson and VanderKooy (1997) reported 16.6 mm TL (15.6 mm SL) to be the size at first maturity for males and 22.9 mm TL (17.6 mm SL) for females in Mississippi.

The objective of this study was to contribute to the understanding of the life history of *Enneacanthus gloriosus* in the western periphery of its range. We anticipated marked differences in life history characteristics in coastal Mississippi compared to more northern locations because of the clear geographic variation in body size and associated life-history differences (*sensu* Ray, 1960; Lindsey, 1966; Atkinson and Sibly, 1997). Specifically, we quantified length-weight and length-age relationships, sex ratio, gonadosomatic index (GSI) and egg diameters and discussed these data in terms of geographic variation.

#### METHODS AND MATERIALS

*Field sampling.*—*Enneacanthus gloriosus* were collected biweekly between October 1995 and October 1996 from Old Fort Bayou, Mississippi, a tidal river of Biloxi Bay on the Mississippi Gulf coast. The 1st 10 fish encountered were collected between 1230 and 1630 h on sampling days with a seine and/or dipnet. Specimens were anesthetized in MS-222, fixed in 10% formalin for 1 wk, flushed with tap water for 24 h and stored in 50% isopropanol. An additional collection of up to five fish per sample was separately fixed and stored in 95% ethanol for otolith aging and marginal increment analysis.

*Length-weight and age relationships.*—Specimens were sexed, blotted to remove excess moisture, weighed (wet weight, WW; 0.001 g) with an Ohaus TP200S electronic balance and measured for both SL and TL with a dial caliper to the nearest 0.1 mm. We used the TL-SL regression equations from this study to convert SL data in Peterson and VanderKooy (1997), Fox (1969) and Hellier (1967) to TL and presented both values where appropriate for comparative purposes.

Procedures used in otolith analysis followed Secor *et al.* (1991). Araldite encapsulated otoliths (two-part epoxy encapsulating compound manufactured by Ciba-Geigy) were cut with an Isomet low-speed saw across the transverse plane and mounted onto microscope slides using thermoplastic cement. All mounted sections were ground with 600 grit sandpaper and polished with 0.3  $\mu\text{m}$  alumina powder until the sulcus formed a sharp point at the primordium. Otoliths were measured along the sulcus from the primordium to each annulus and the ventral margin with an ocular micrometer at a magnification of 400 $\times$ . Ages follow the convention of using arabic letters as in DeVries and Frie (1996) and were verified by two independent readers.

The same otoliths used to age the fish were used for marginal increment analysis; values ( $\bar{x} \pm \text{SE}$ ) were plotted by month to estimate the timing of annular ring deposition. This analysis consisted of measuring the distance along the sulcus from the outer edge of the last ring to the margin of the otolith (Ross, 1988). A length-age structure was constructed using fish collected in the biweekly samples. After a subsample of fish was aged ( $n = 76$ ), we used the  $\bar{x} \pm 95\%$  TL confidence intervals (CI) of those fish to estimate TL ranges for each age class for all remaining fish. If a fish's TL overlapped adjacent age intervals, we divided the number of overlapping fish equally between each age interval. Fish that could not be placed into any age interval (those that fell between the adjacent 95% CI) were excluded from this analysis ( $n = 32$ ). A total of 284 fish were used to estimate the length-age structure.

*Reproduction.*—Gender was determined by observing the gross morphology of the gonads. We classified ovarian stage of maturity following Knight and Ross (1992): (1) latent (LA); (2) early maturing (EM); (3) late maturing (LM); (4) mature/ripe (MA), and (5) spent (SP). Ova of each female were sorted by color and shape into three size classes. Class 1 ova were transparent with a visible white nucleus, were well attached to surrounding tissue, and

were generally the smallest ova in the ovary. Class 2 ova were opaque, slightly misshaped from contact with other ova, uniformly white in color (no oil drops) and were larger than class 1 ova. Class 3 ova were opaque, yellow, had oil droplets that were clearly visible, were nearly free of any connection to tissues or other ova, were nearly perfectly round and smooth, and were the largest of all ova. We then counted all ova per size class and reported results in relation to female body size. In females with late maturing, mature/ripe and spent ovaries, ova diameters of the 10 largest ova (class 3) were measured with an ocular micrometer in the longest and shortest dimensions and the values were averaged. Testicular maturity was categorized as latent (LA) or mature (MA) following Parrish *et al.* (1991). Fish  $\geq 20$  mm SL ( $\geq 26.1$  mm TL) were selected to calculate the gonadosomatic index [GSI; gonadal weight divided by eviscerated somatic weight multiplied by 100 (Crim and Glebe, 1990)] to assure that only mature fish were used. Gonadal and eviscerated somatic tissue samples were dried for 24 h and 48 h, respectively, to a constant weight at 60 C (Baker and Heins, 1994). Tissues were allowed to cool in a desiccator and eviscerated somatic tissue was weighed (dry weight) to the nearest 0.001 g and the gonadal tissue weighed (dry weight) on a Kahn electrobalance to 0.0001 mg.

*Statistical procedures.*—Least-squares linear regression was used to compare SL and TL, TL and dry weight (DW, both variables  $\log_{10}$  transformed), age and TL, and GSI and WW (somatic wet weight – gonad wet weight) for males and females separately; the latter comparison was used to validate the use of GSI as an index of spawning preparedness. Analysis of covariance (ANCOVA) was used to test for differences in TL and dry weight between males and females with TL as the covariate. The slopes and y-intercept parameters from the TL and dry weight regressions of males and females were used to estimate their power function if the TL-dry weight relationships were significantly different. If the relationships did not differ, male and female data were pooled. The power function is  $W = aL^b$ , where W is dry weight, L is TL, and  $a$  (back-transformed y-intercept) and  $b$  (slope) are the parameters (Anderson and Neumann, 1996). The ratio of males to females was compared to a 1:1 sex ratio by a  $\chi^2$  Goodness of Fit test. All statistical procedures were conducted with SPSS PC+ statistical software (Version 5.0, SPSS Inc., Chicago, Ill.) and tests were deemed significant if  $P < 0.05$ . Pending the outcome of the relationship between GSI and WW of males and females, GSI ( $\bar{x} \pm SE$ ) was plotted by month to indicate spawning season.

## RESULTS

Biweekly collections produced 316 *Enneacanthus gloriosus* ranging from 14.2 to 44.0 mm TL (Fig. 1). The slopes of the TL and dry weight relationship between males and females were parallel (ANCOVA,  $df = 1$ ,  $F = 1.12$ ,  $P = 0.29$ ), and there was no difference in the y-intercepts (ANCOVA,  $df = 1$ ,  $F = 1.01$ ,  $P = 0.32$ ); thus the data were pooled for further analysis. The pooled relationship of TL to dry weight was described by  $\log_{10} DW = -6.15 + 3.40 \log_{10} TL$  and was significant ( $df = 235$ ,  $r^2 = 0.86$ ,  $P < 0.0001$ ). The power function was  $W = 7.04^{-7} L^{3.4022}$ . The pooled relationship between SL and TL was described by the equations  $SL = 0.504 + 0.749 (TL)$  and  $TL = -0.324 + 1.321 (SL)$  and each was significant ( $df = 314$ ,  $r^2 = 0.99$ ,  $P < 0.0001$ ).

Marginal increment analysis showed the largest marginal increments occurred during August and September for age 1 fish, and during August and October for age 2 fish (Fig. 2). The minimum marginal increments occurred from November through April for both ages, which we consider the period of annulus formation (Fig. 2). There were not enough fish age 3 or 4 for adequate examination. Ages varied from 0 to 4 (total  $n = 76$ ) with a large overlap in the length-at-age due to small sample sizes as well as the potential for a protracted reproductive season. Most fish were age 1 and 2 ( $n = 58$ ), and no females occurred in the

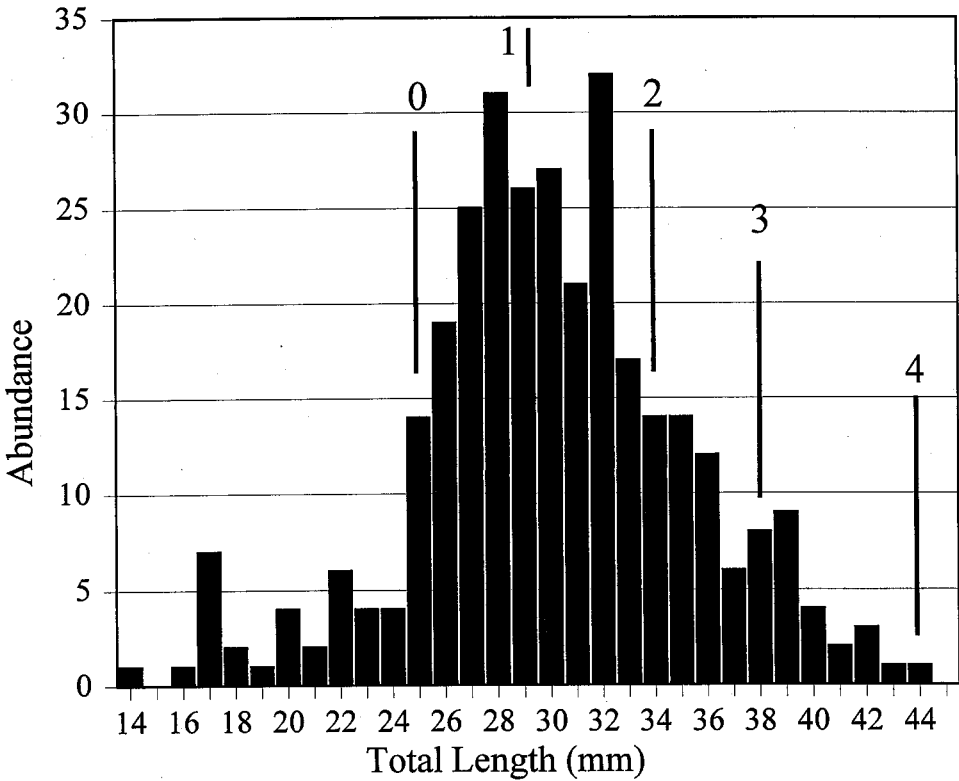


FIG. 1.—Abundance of 316 *Enneacanthus gloriosus* (pooled genders). Mean size at age indicated by numbered vertical lines

age 0 group (Fig. 3). The mean TLs for ages 0–4 were  $25.9 \pm 2.2$  ( $n = 8$ ;  $\bar{x} \pm SE$ ),  $28.7 \pm 0.9$  ( $n = 29$ ),  $33.5 \pm 0.9$  ( $n = 29$ ),  $38.1 \pm 1.4$  ( $n = 9$ ) and  $44.0$  mm ( $n = 1$ ), respectively. The relationship between age and TL for males was  $\text{Age} = -1.317 + 0.08714 (\text{TL})$  ( $df = 38$ ,  $r^2 = 0.43$ ,  $P < 0.05$ ; Fig. 3), and for females was  $\text{Age} = -1.647 + 0.106 (\text{TL})$  ( $df = 31$ ,  $r^2 = 0.40$ ,  $P < 0.05$ ; Fig. 3). The slopes and the y-intercepts of the age-TL relationships between males and females were not different ( $P > 0.05$ ).

The sex-ratio did not differ significantly from 1:1 ( $\chi^2 = 0.051$ ,  $P > 0.05$ ). There was no relationship during the reproductive season (April–September) between GSI and WW for males categorized as MA ( $df = 37$ ,  $r^2 = 0.01$ ,  $P > 0.05$ ) or for females categorized as EM, LM and MA ( $df = 35$ ,  $r^2 = 0.05$ ,  $P > 0.05$ ). Thus, the use of GSI as an indicator of spawning preparedness was warranted. Mean GSI values were highest between April and August, peaking at 0.6% for males and 8.8% for females in May (Fig. 4). The initial increase for males and females followed increasing water temperature above 15 C, but GSI decreased while water temperature remained around 27 C (Fig. 4). The maximum individual GSI for males was 0.8% (May) and 15.8% (June) for females. For males and females, mean GSI declined during July, followed by a second, lower mean peak in August ( $\delta = 0.3\%$  and  $\text{♀} = 5.4\%$ ), and subsequent low values for the rest of the year (Fig. 4). This July decline is further illustrated with several males (Table 1) and one female (Table 1) being categorized

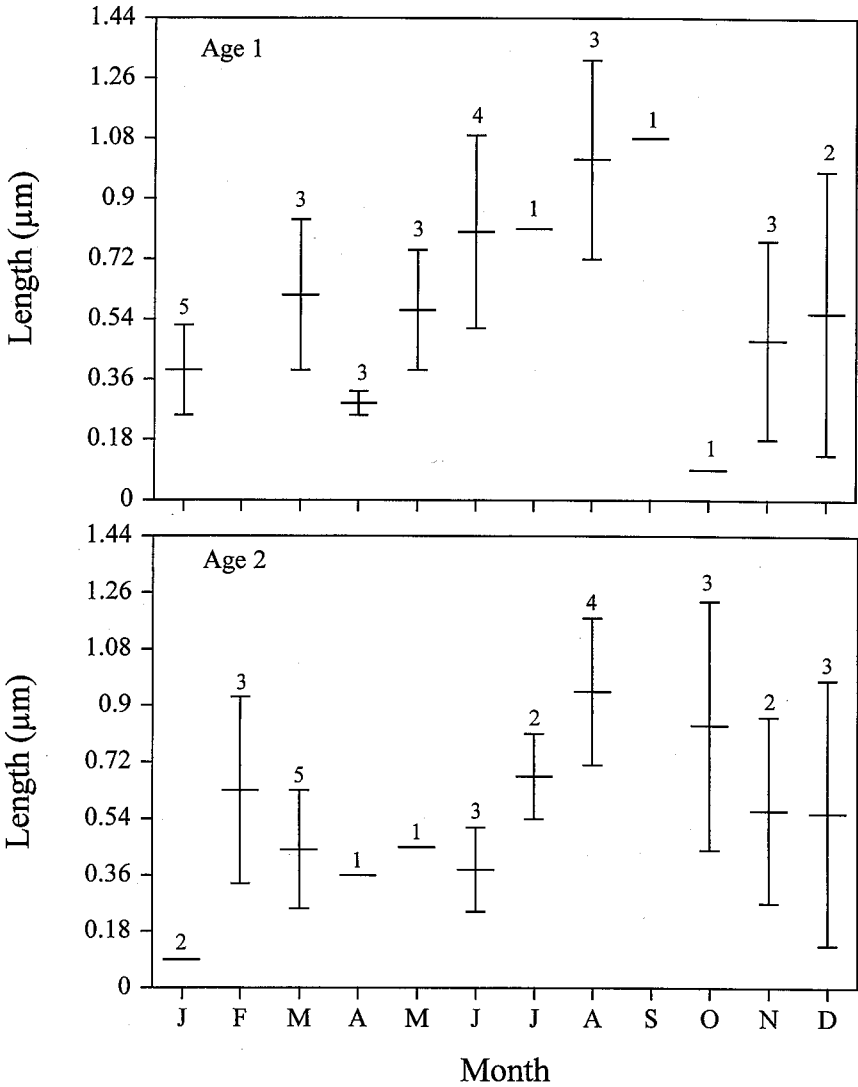


FIG. 2.—Marginal increment of *Enneacanthus gloriozus* otoliths by month. Values are presented in  $\mu\text{m}$  ( $\bar{x} \pm \text{SE}$ ). Numbers above values are sample sizes

as LA and from the decrease in percentage of reproductively active females (Table 1). Males matured as early as April and were LA after August (Table 1). Several females were EM as early as January, and by March all females were EM (Table 1). The beginning of the spawning season was in mid-April.

Clutch size of individual MA females varied from 42 to 216 mature ova (mean = 117.2;  $n = 37$  fish), with no correlation between the number of mature ova and TL ( $df = 35$ ,  $r^2 = 0.07$ ,  $P > 0.05$ ) for fish collected between April and September or for total ova numbers (all three classes) and TL ( $df = 35$ ,  $r^2 = 0.00$ ,  $P > 0.05$ ). Class 1 ova (immature) diameter

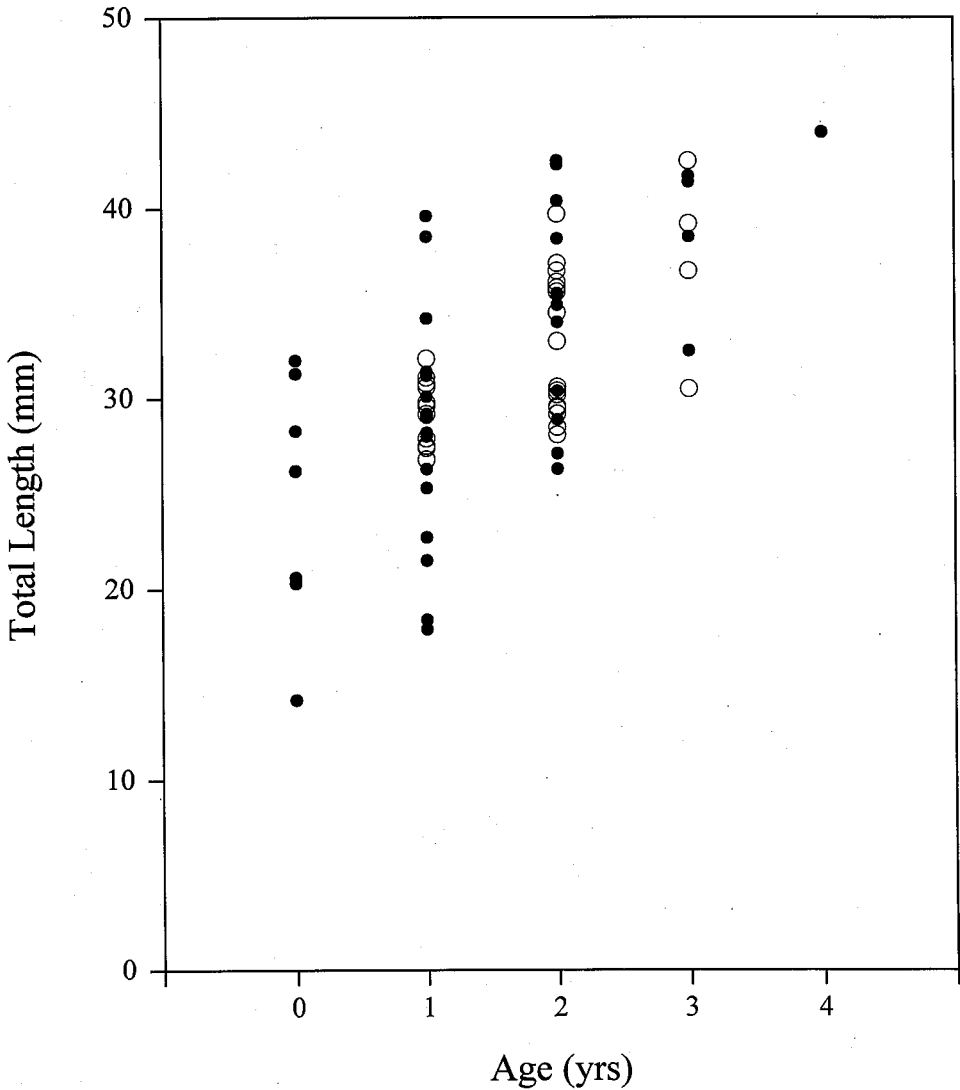


FIG. 3.—Relation of total length and age of male (shaded circle:  $n = 40$ ,  $r^2 = 0.43$ ,  $P < 0.01$ ) and female (open circle:  $n = 33$ ,  $r^2 = 0.40$ ,  $P < 0.01$ ) *Enneacanthus gloriosus*

ranged from 0.02 to 0.16 mm ( $n = 37$  fish; 19,391 total ova), class 2 ova diameter ranged from 0.07 to 0.48 mm ( $n = 37$  fish; 2,806 total ova) and class 3 ova diameter ranged from 0.56 to 0.83 mm ( $n = 37$  fish; total 4,337 ova). The mean total number of ova was highest at the beginning of the reproductive season, and reached a second, lower peak through July and August, while maturing ova numbers fluctuated throughout the season (Fig. 5). Finally, class 3 ova percentages were low in April but increased throughout the summer (Fig. 5) indicating recruitment of immature ova into mature (class 3) ova. This pattern of

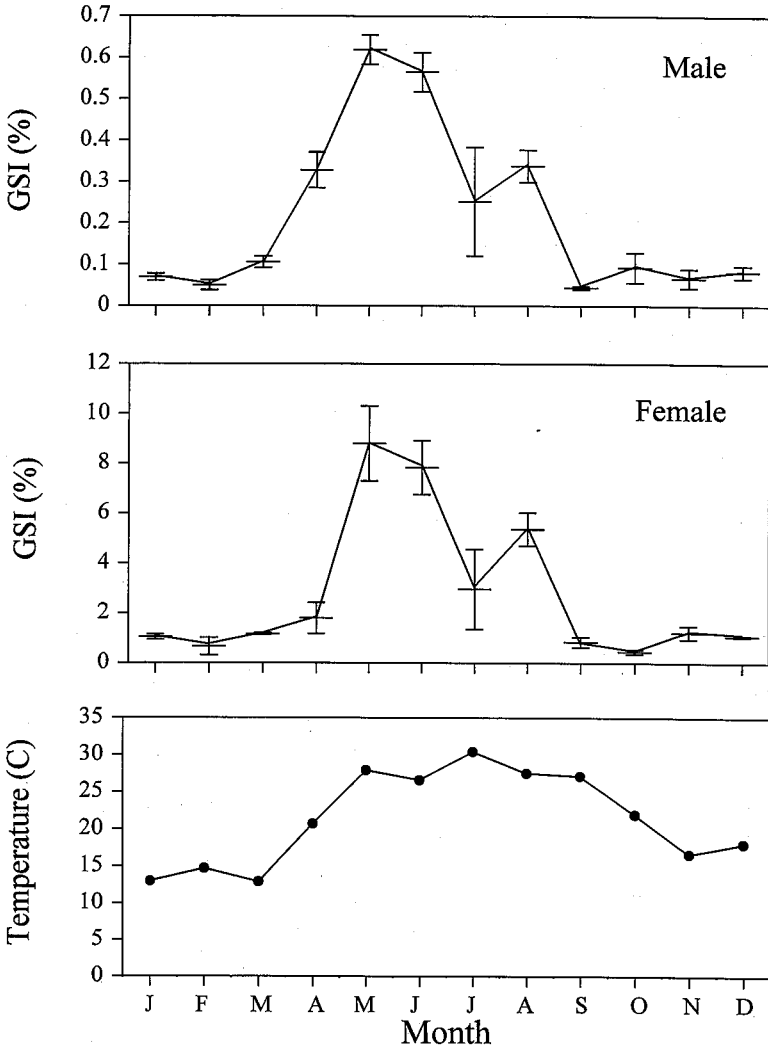


FIG. 4.—Monthly GSI for *Enneacanthus gloriosus* showing  $\bar{x} \pm SE$  for males (n = 114) and females (n = 124). Bottom panel shows water temperature

mature and developing ova being present in the same female throughout the season indicates multiple batch spawning.

DISCUSSION

Various aspects of the life history of the *Enneacanthus gloriosus* population in Mississippi differ substantially from those of E-coast populations (Hildebrand and Schroeder, 1928; Breder and Redmond, 1929; Raney, 1965; Occhiogrosso and Goodbred, 1981), and to a lesser degree from those in central Florida (McLane, 1955; Hellier, 1967; Fox, 1969). For example, maximum size of *E. gloriosus* collected in this study was 51.2 mm TL (38.6 mm

TABLE 1.—Number of fish per testicular stage by month (1995 n = 22, 1996 n = 92) and ovarian stage by month (1995 n = 27, 1996 n = 97) of *Enneacanthus gloriosus* taken over a 1-yr period. Percentages of females that are reproductively active (EM, LM and MA) each month are given below

Gender	Stage	1995			1996									
		Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct
Male	LA	5	7	10	17	6	8	7				3	10	5
	MA							3	12	9	2	10		
Female	LA	5	6	6	3	2		1			1	2	3	3
	EM				3	2	19	5	1		1			
	LM							2		3				
	MA							2	7	8	2	14	1	
	SP												6	2
	%	0	0	0	50	100	100	90	100	100	75	887	10	0

SL) and, in a spatially wider ranging study in Mississippi, was 58.4 mm TL (44.5 mm SL) (Peterson and VanderKooy, 1997). East coast and S Florida specimens reach 85 mm TL (Hildebrand and Schroeder, 1928; Breder and Redmond, 1929; Gunter and Hall, 1965), whereas central Florida specimens reach 77 mm TL (McLane, 1955; Hellier, 1967; Fox, 1969). Additionally, population age structure also differs geographically. In New Jersey, *E. gloriosus* reached a maximum of age 5 (55–71 mm SL, Breder and Redmond, 1929) but in Mississippi, fish reached only age 4 (33.5 mm SL). The length-age structure of the Mississippi *E. gloriosus* population indicated that age 0 through 3 fish represented 81.0% of the 284 total fish examined, whereas age 0 through 3 fish from central Florida represented 93.0% of the 255 total fish collected (Fox, 1969). These data suggest that age 1 through 3 fish dominated both populations, and in both studies fish age 4 either did not occur or were not abundant. Fox (1969) suggested most fish > age 3 were removed from the population in his system, and *E. gloriosus* in our system exhibited a similar pattern of few large fish.

The timing of annular increment formation in Mississippi *Enneacanthus gloriosus* was protracted with age 1 fish exhibiting reduced marginal increments from October to May and age 2 fish exhibiting reduced marginal increments from January to June. This pattern is complicated because of small sample sizes each month, which caused considerable variation in the measured increment. However, since temperature is important in slowing growth and causing annulus formation (Ross, 1988), and because water temperatures during this study did not drop below 13 C, it is possible that the Mississippi *E. gloriosus* did not form distinct annuli. In fact, temperature at the terminus of Old Fort Bayou with Biloxi Bay has not fallen below 11.2 C since 1992. Daily ring formation has been shown to continue if temperature was above 10 C in bluegill *Lepomis macrochirus* (Taubert and Coble, 1977) and 12–15 C in largemouth bass, *Micropterus salmoides* (Taubert and Tranquilli, 1982). In both species, lower temperatures stopped somatic growth and caused ring formation. Assuming that temperature similarly influences growth in *E. gloriosus*, growth might not have slowed to the point where a distinct annulus was formed.

*Enneacanthus gloriosus* in Mississippi exhibited a growth advantage in the 1st yr of life compared to fish in Florida and New Jersey, but by age 3 Mississippi fish were generally smaller than Florida and New Jersey fish (Table 2). A longer growing season, milder winters and faster growth during the 1st yr of life allow age 0 fish to achieve a larger body size and sexual maturity by the end of the 1st yr compared to high latitude populations. It is likely



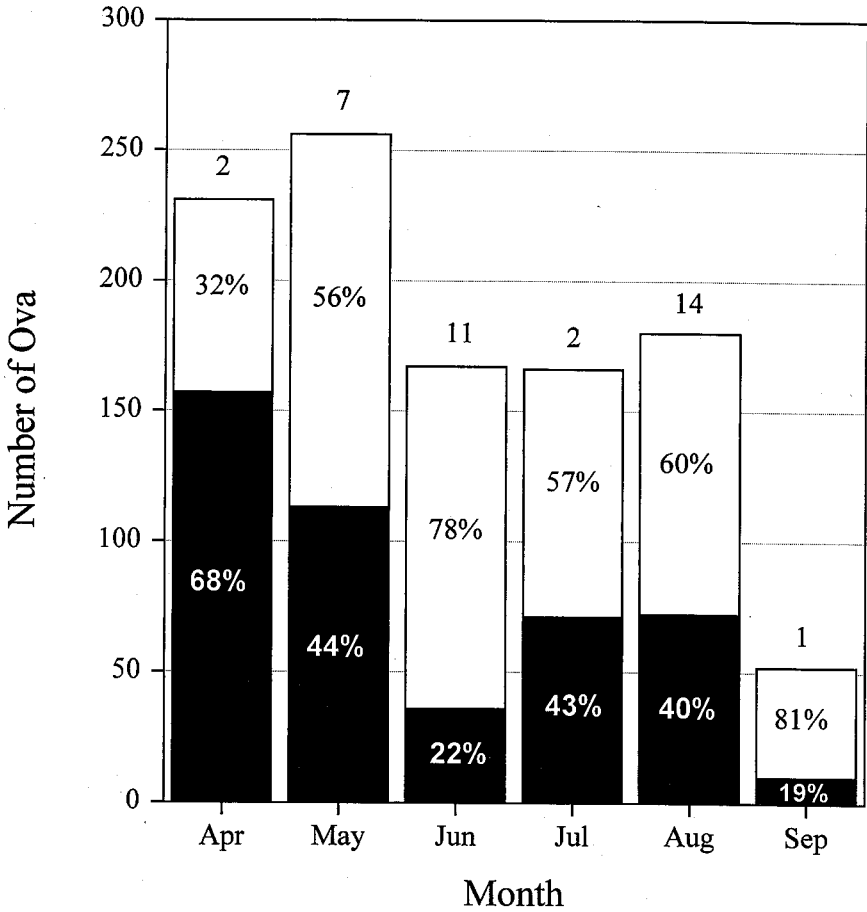


FIG. 5.—Clutch size of 37 gravid *E. gloriosus* averaged by month. Number of individuals are shown above each bar and values within each histogram represent % of class 3 ova (open) and class 1 + 2 ova (black)

TABLE 2.—Mean SL by age of *Enneacanthus gloriosus* from Mississippi, Florida and New Jersey populations

Age	Mississippi (Present study)	Florida Fox (1969)	New Jersey (Breder and Redmond, 1929)
0	19.2	16.7	~15.0
1	22.0	26.0	~30.0
2	25.6	35.7	
3	29.0	41.8	~40–50
4	33.5	~59.0	
5			~62.0

that the growth rate of the Mississippi *E. gloriosus* decreased with the onset of maturity; fish 18–19 mm SL (23.5–24.8 mm TL) corresponding to age 0 began investing energy into gonadal development (Peterson and VanderKoooy, 1997; this study). Compared to the northern populations, survival in the warmer Mississippi climate requires less investment into somatic growth. Thus a greater portion of resources can be devoted to reproduction, resulting in a higher reproductive investment earlier in life as has been shown in other Gulf Coast species (Brown-Peterson and Thomas, 1988; Peterson-Curtis, 1996).

Fishes with a wide geographical distribution, as *Enneacanthus gloriosus*, while often differing in body size and growth, also differ in reproductive life history traits (Brown-Peterson and Thomas, 1988; Jonsson and L'Abée-Lund, 1993; Peterson-Curtis, 1996; Power and McKinley 1997). These clinal patterns of variation have been attributed to such factors as density-dependent mechanisms, temperature, variable energetic costs of migration and spawning and variable prey availability (Ray, 1960; Edwards, 1984; Shuter and Post, 1990; Jonsson and L'Abée-Lund, 1993). In New Jersey and New York, *E. gloriosus* had a protracted spawning season, extending from late spring through summer (Breder and Redmond, 1929; Occhiogrosso and Goodbred, 1981). In Mississippi, spawning occurred from mid-April through September, and in Florida spawning occurred between April and October (McLane, 1955; Hellier, 1967). The length of the spawning season is longer in the south due to the warmer water temperature coupled with a long daily photoperiod (~15 h) that Harrington (1956) found was required to initiate gametogenesis in the banded sunfish, *E. obesus*. In comparison, most centrarchids (Breder, 1936) and other freshwater species (Hubbs, 1985) in northern latitudes spawn during a shorter season, generally in spring and early summer. *Enneacanthus gloriosus* in Mississippi reached 50% maturity during their 1st summer of life (23.4–24.8 mm TL, 18–19 mm SL; Peterson and VanderKoooy, 1997; this study) whereas in central Florida, Fox (1969) noted 1st-yr females with maturing ova before their first spawn were ~21.7 mm TL (~16.7 mm SL). In contrast, *E. gloriosus* in New York and New Jersey spawn in their 2nd yr of life between 40–50 mm SL (Breder and Redmond, 1929; Raney, 1965; Occhiogrosso and Goodbred, 1981). An interesting hypothesis, compatible with life history theory, indicates that an increased emphasis on reproduction (early maturity and increased spawning frequency) leads to increased mortality in adults (Gerking, 1959; Shepherd and Grimes, 1983). This hypothesis may explain the lack of larger and older fish relative to early maturity in Mississippi *E. gloriosus* as noted above. The most parsimonious explanation of this observed age/maturity pattern is temperature, as described by Ray (1960), Lindsey (1966), DiMichele and Westerman (1997), and Atkinson and Sibly (1997). Temperature is particularly relevant since *E. gloriosus* in coastal Mississippi are not extremely abundant, do not migrate for reproduction and prey availability is probably not limiting since diet data were comparable with data from other latitudes (Snyder, 1997).

The Mississippi population of *Enneacanthus gloriosus* is a multiple batch spawner, as males and females had two distinct peaks in gonadal maturity between mid-April and September. Furthermore, ripe eggs were found during every month of the spawning season. The presence of various staged ova throughout the spawning season and no spent ovaries until late August confirms Fox's (1969) hypothesis that *E. gloriosus* release a few eggs at a time, thus never leaving a spent ovary until the end of the season. This has been observed in captive *E. obesus*, with 115 spawning acts involving egg deposition observed during a 26-day period (Harrington, 1956).

Mature (class 3) ova diameter of preserved Mississippi *Enneacanthus gloriosus* was on average 0.68 mm (range of  $\bar{x}$  values = 0.62–0.71 mm; 21.7–29.9 mm TL fish) which is similar to the 0.5 mm diameter ova (14.7–28.2 mm TL fish) of preserved fish from central Florida

reported in McLane (1955). These data differ from the 0.9-mm diam of hydrated eggs from New Jersey fish (Breder and Redmond, 1929). This difference is likely due to preservation-related shrinkage in our study and McLane's (1955), and the fact that oocytes in Breder and Redmond's (1929) study were recently laid on vegetation and thus were hydrated and larger. Additionally, mature (class 3) ova number in Mississippi fish ranged from 42–216 ( $\bar{x}$  = 117.2) per female which was different than Fox (1969) in central Florida who indicated 67–509 mature ova per ovary and McLane (1955) who reported 84–635 total ova per female ( $\bar{x}$  = 220) in E-central Florida. However, the total number of ova in Mississippi fish ranged from 52–1929 per female ( $\bar{x}$  = 702) which is more comparable to evidence in McLane (1955). The differences in egg numbers is likely related to differences in female body size among studies, with Mississippi having the smallest maximum body size (Peterson and VanderKooy, 1997). Occhiogrosso and Goodbred (1981) noted that fish in New York had 200 ova per female but reported no size range or developmental stage data for ova counts. Although we found no relationship between mature (class 3) ova number and TL or total ova number and TL, Fox (1969) concluded that the number of mature ova increased with age (TL and age were highly correlated). Fox's study, however, was conducted before the spawning season, between January and April, after which fluctuations in ova number would have been noticeable in the summer, as seen in our ova numbers.

Life history characteristics for *Enneacanthus gloriosus* in Mississippi vary markedly from E coast, and to a lesser degree, from Florida populations. These data suggest latitudinal variation with maximum body size, age, mature ova size and length at maturity being reduced and spawning season being longer than New Jersey fish. All of these life history traits were, however, more similar to those in central Florida *Enneacanthus gloriosus* than in New Jersey. Moreover, maximum body size in Mississippi populations was at the extreme lower range of body size noted in all geographic locations where data are available. Future research needs to focus on delineating egg-body size relationships and age or size at first maturity differences as well as the underlying genetic mechanisms associated with these geographic differences throughout their natural range.

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