Reproduction, Fecundity, Sexual Dimorphism and Sex Ratio of Etheostoma fonticola (Osteichthyes: Percidae)

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ABSTRACT: *Etheostoma fonticola* is an endangered species of fish which spawns year-round in the relatively constant temperature headwaters of the San Marcos River and in Spring Lake (impounded origin of the river), Hays Co., Texas. However, the species appears to have two spawning peaks, one in August and the other in late winter to early spring. Proposed explanations for this observed spawning periodicity are a slight increase in water temperature and/or a decrease in flow.

Ripe ovaries of preserved *Etheostoma fonticola* contain three distinct classes of ova based on their size and appearance. The number of mature ova (Size Group I) is positively correlated with total length of the fish while the mean diameter of mature ova is not positively correlated. *Etheostoma fonticola* provides no parental care to the ova and has very low fecundity (mean fecundity was 19).

Sexual dimorphism is evident in the shape and size of the genital papillae and the pelvic fins and in the intensity of body coloration.

The sex ratio of *Etheostoma fonticola* is 1.39:1.00 (M:F).

INTRODUCTION

The fountain darter *(Etheostoma fonticola)* is an endangered species of fish which occupies vegetated habitats in the headwaters of the San Marcos and Comal rivers, S-central Texas, and has recently been introduced into a refugium for endangered species at the Dexter National Fish Hatchery, New Mexico (Schenck and Whiteside, 1976).

Little has been published concerning the reproduction of this small, bottom-inhabiting fish. Hubbs and Strawn (1957a) and Hubbs (1959) used *Etheostoma fonticola* as experimental animals in hybridization studies; Strawn (1955, 1956) described various ecological aspects of this species in his papers on breeding and raising three Texas darters; and Strawn and Hubbs (1956) described a method of stripping the ova and sperm from *E. fonticola.* The objectives of this study were: (1) to determine the spawning times, fecundity and sex ratio of the species; (2) to correlate fecundity with fish size and parental care of ova; (3) to assess the relationship between ova size and fish size; and (4) to describe the sexual dimorphism of *E. fonticola.*

MATERIALS AND METHODS

Collections. — Monthly collections (March 1973 through April 1974) were taken with a fine-mesh dip net from an area directly adjacent to the Aquarena Springs Hotel in Spring Lake and from five representative stations in the upper 4.8 km of the San Marcos River.

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These collections sampled the entire range of *Etheostoma fonticola* in the San Marcos River watershed. The specimens were preserved in 10% formalin.

The origin of the San Marcos River is impounded to form Spring Lake (18 ha), which receives most of its water from constant temperature springs of the Edwards Aquifer. Based on 12 monthly water-temperature determinations made during the study period, Spring Lake had a mean of 21.8 C, range 21.0-22.0 C, while the water 4.8 km downstream from Spring Lake Dam had a mean of 22.8 C, range 20.6-24.9 C. For a complete description of the upper San Marcos River watershed and collecting stations, *see* Schenck (1975).

Analytical methods.—The relationship between body weight and the weight of the left ovary was used to determine seasonal patterns of ovarian development in females. Only females 24.0 mm or longer total length were used in this analysis, because only they contained mature ova ($\geqslant$ 1.00 mm diam; *see* FECUNDITY). The female and her left ovary were weighed separately to the nearest 0.01 mg on a Mettler single pan balance after blotting on paper toweling. The left ovary weight was then converted to a percentage of the body weight. Fish which contained ovaries too small to accurately separate into the right and left ovary were omitted.

After weighing, the left ovary was split into several pieces and shaken violently in a vial containing 70% ethanol. The separated ova (mature and immature) were counted, and the count was doubled to represent both ovaries. Fecundity of each fish was then expressed as the doubled count of mature ova.

The diameter of each separated ovum was measured to the nearest 0.01 mm with an ocular micrometer. The mean ova diameter for each fish and the mean ova diameter for all fish collected each month (mean monthly ova diameter) were then calculated and used as an indicator of ovarian development. If the left ovary contained no separated ova, the diameter of the largest ovum was used as the mean

The relationship between the square root of the total length of the male and the width of his left testis was used to determine seasonal patterns in testicular development. Only males 24.0 mm or longer in total length were used because females in this size range were used and because the minimum size of mature males was unknown. The width of the left testis was measured to the nearest 0.01 mm with an ocular micrometer and then converted to a percentage of the square root of the total length.

RESULTS AND DISCUSSION

Data from fish collected in Spring Lake and in the San Marcos River were initially analyzed separately but were later combined because of insufficient data from Spring Lake.

Spawning times.—*Etheostoma fonticola* had two temporal peaks of ova development, one in August and the other in late winter to early spring (Fig. 1); therefore, they appear to have two major spawning periods annually. The monthly percentages of females with ovaries containing at least one mature ovum also demonstrated the two annual spawning peaks (Fig. 2). However, females containing at least one mature ovum were collected throughout the year (Fig. 2), which suggested year-round spawning. The ovary weight/body weight relation-

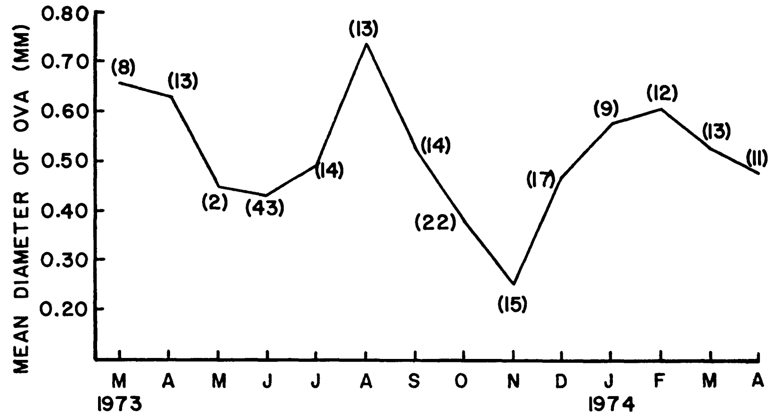

Fig. 1.—Mean monthly diameter of ova from *Etheostoma fonticola* 24.0 mm or greater total length. Number of specimens examined each month is given in parentheses

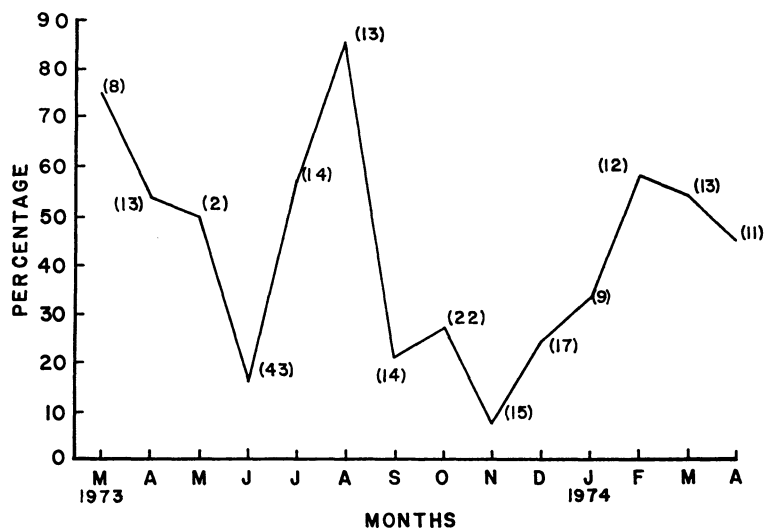

Fig. 2.—Monthly percentages of *Etheostoma fonticola* 24.0 mm or greater total length which had at least one mature ovum. Number of specimens examined each month is given in parentheses

ship (Fig. 3) and the testis width/square root of total length relationship (Fig. 4) also indicated the two spawning periods.

Most other darters spawn in the spring or early summer (Braasch and Smith, 1967; Fahy, 1954; Jaffa, 1917; Karr, 1964; Lachner *et al.*, 1950; Lake, 1936; Mount, 1959; New, 1966; Page, 1974; Page and Smith, 1970, 1971; Petravicz, 1936; Petravicz, 1938; Raney and Lachner, 1939; Reeves, 1907; Scalet, 1973; Speare, 1965; Thomas, 1970; Tsai, 1972; Winn and Picciolo, 1960). However, populations of *Etheostoma lepidum* and *E. spectabile*, which live in areas with slight annual water temperature variation, have extended their breeding periods up to 10-12 months (Hubbs and Strawn, 1957b; Hubbs *et al.*, 1968). Since *E. fonticola* also lives in a constant temperature environment, it is not surprising that it spawns year-round. Strawn (1955) also reported year-round spawning by *E. fonticola* in the San Marcos River but provided no data to support his conclusion.

There are at least two explanations for the observed bimodal spawning periodicity of *Etheostoma fonticola*, but since both are based on only 1 year's data, they are speculative. First, the two spawning peaks paralleled an increase in mean water temperature for the study

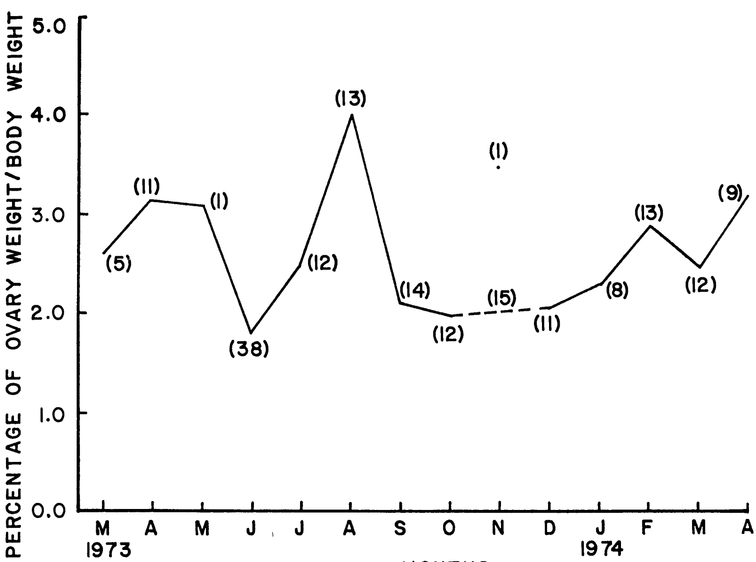

Fig. 3.—Monthly changes in ovary weight/body weight relationship for *Etheostoma fonticola* 24.0 mm or greater total length. Number of specimens examined each month is given in parentheses. Only one fish collected in November 1973 contained ovaries large enough to weigh; therefore, this one fish was not considered representative of the November collection and was omitted from the curve

area (Table 1). This suggested that the warming trends triggered spawning or the optimal temperature range for spawning was narrower than the relatively small temperature fluctuation of the study area. Hubbs and Strawn (1975b), in laboratory experiments, found fecundity of *E. lepidum,* which also lives in constant temperature streams of S-central Texas, varied with water temperature with an optimal temperature for egg production between 20 and 23 C. This 3-deg tempera-

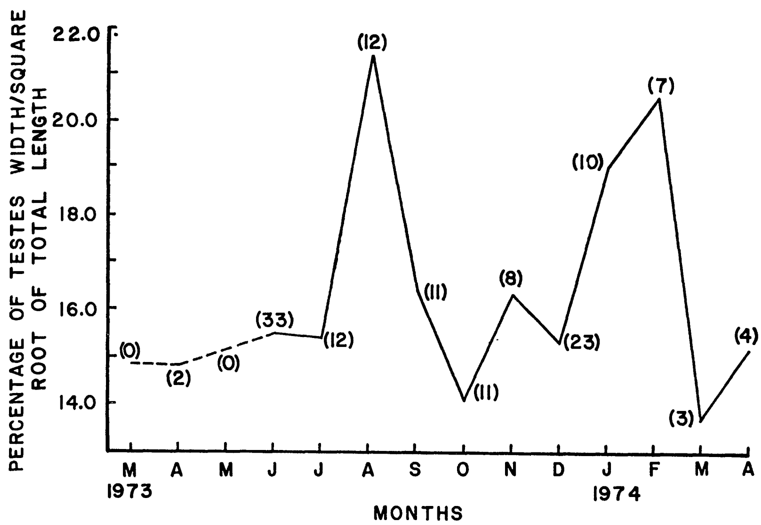

Fig. 4.—Monthly changes in the testes width/square root of total length relationship for *Etheostoma fonticola* 24.0 mm or greater total length. No males in this size range were analyzed during March and May 1973. Number of specimens examined each month is given in parentheses

TABLE 1.—Average monthly water temperature and flow of the upper San Marcos River, Hays Co., Texas. Flow data is from the Edwards Bulletin (1973-74)

Month	Year	Flow (ft^3/sec)	Temperature (C)
March	1973	215	23.1
April	1973	233	23.5
May	1973	220	22.6
June	1973	230	22.8
July	1973	240	23.2
August	1973	201	24.8
September	1973	198	22.2
October	1973	300	22.6
November	1973	277	21.6
December	1973	225	21.1
January	1974	216	20.6
February	1974	185	20.7
March	1974	185	22.0
April	1974	164	21.9

ture range was greater than the annual range in upstream waters of our study area. However, *E. lepidum* occurs in areas other than those with a constant water temperature. Therefore, *E. fonticola* may have a much narrower temperature range for optimal reproduction. Second, the flow of the San Marcos River may have contributed to the observed spawning periodicity. There was an indication of an inverse correlation between the spawning peaks and flow (Table 1). Therefore, it is possible that a decrease in flow triggered spawning or provided more spawning habitat. Young fish, as well as adults, were consistently collected in heavily vegetated, backwater areas of the river where the flow was negligible (Schenck and Whiteside, 1976). It is not known whether spawning occurred in these specific areas but Strawn (1956) reported that *E. fonticola* spawns on vegetation.

Other factors such as food availability, light intensity and light duration have been implicated in the spawning periodicities of fishes. The monthly percentages of *Etheostoma fonticola* collected throughout the study period which had food in their stomachs (Schenck, 1975) were not correlated with the observed spawning periodicity. Therefore, availability of food apparently was not conducive to the spawning peaks. Also, light duration and intensity were different for the two spawning peaks which indicated that they probably were not contributory to the observed peaks. Hubbs and Strawn (1975b) found that light duration and intensity did not appear to affect fecundity of *E. lepidum.*

Fecundity.—Ripe ovaries of preserved *E. fonticola* contained three distinct classes of ova: Class I (1.00-1.40 mm), Class II (0.65-0.99 mm) and Class III (0.05-0.64 mm). Class I ova were yellow with a relatively large yellow-orange oil globule and were considered mature. The outer boundary of the ova encapsulated the yellow yolk material and was transparent. The ova were consistently pinched in on one side, were very hard, and had flattened sides where they adhered to each other. Class II ova were also yellow because of yolk material but contained no distinct oil globule, were not as hard as Class I ova, and did not have flattened sides. Class III ova were similar to Class II ova but were white because yolk was absent.

Most darters have rather low reproductive capabilities. Previous studies have shown that the ova complement of eight species of *Etheostoma* ranged from 50 to ca. 500 (Raney and Lachner, 1939; Petravicz, 1936; Page, 1974; Speare, 1965; Scalet, 1973; Lake, 1936; Hubbs *et al.,* 1968). Based on 74 *E. fonticola* which contained mature ova, the mean fecundity was 19, which is even lower than in the other darters. This low fecundity is probably compensated for by repeated spawnings of small groups of eggs throughout the year. It is not known how many ova are spawned annually by each *E. fonticola,* but it is probably considerable.

Generally, smaller female *Etheostoma fonticola* contained fewer mature ova than larger females (Fig. 5). This positive correlation was significant ($\alpha = 0.01$; 72 df) according to the Pearson productmoment correlation coefficient (Sokal and Rohlf, 1969). A positive correlation between mature ova number and fish size is common among fishes (Vladykov, 1956; Hoar, 1957; Rounsefel, 1957), but the underlying limiting factors which determine the correlation are probably different for different species according to their reproductive habits. Two such limiting factors are available coelomic space and nutrition. The fecundity of fishes which spawn only once in their lifetime would probably be limited by coelomic space restrictions. Fishes with this reproductive habit would have ample time prior to the reproductive season to store the necessary metabolites for ova production. In fact, nutritionally they would probably be capable of producing a greater volume of ova than the available coelomic space would allow. Therefore, space rather than nutrition would limit ova production. Conversely, the fecundity of fishes which spawn continuously throughout the year would probably be limited by nutritional requirements. In this case the females would not be able to store the necessary nutrients for ova production prior to spawning but would have to absorb the nutrients during the spawning season. Therefore, the amount of available nutrients which could be converted into ova would limit fecundity. Since the nutrients must be absorbed through the alimentary tract before they can be converted into ova, the surface area of the tract could limit ova production. Based on the exponential relationship of an increase in ova number with an increase in fish length, Hubbs *et al.* (1968) indicated that digestive absorptive surface

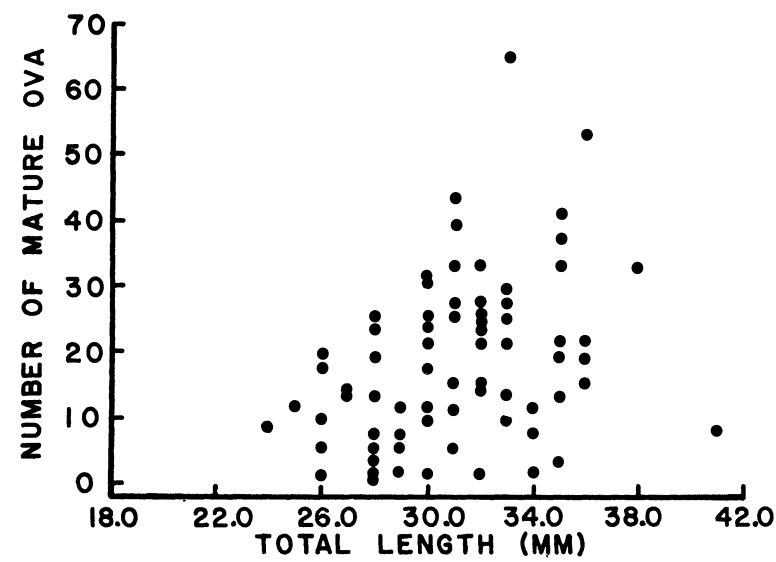

Fig. 5.—Number of mature ova from both ovaries (fecundity) of *Etheostoma fonticola* as a function of total length. Fish without mature ova were omitted

was apparently more limiting than coelomic space in *E. spectabile* and *E. lepidum*. It is suspected that the fecundity of *E. fonticola* is also limited by absorptive surface area, but adequate data were not available for conclusive evaluation. The fecundity of fishes which have a relatively short spawning season each year would probably be limited by a combination of nutritional and coelomic space requirements. Williams (1959), in his study of four spring-spawning darters, indicated that food may be the limiting factor for ova production up to a certain point; but beyond that point the mechanical restrictions on the amount of space in the body cavity, and the necessity of maintaining locomotor functions at a reasonable level of efficiency probably become the limiting factors.

Variation in the number of mature ova in any 1.0-mm interval in total length of *Etheostoma fonticola* was evident (Fig. 5). This variation could have been caused by seasonal fluctuations in fecundity or some fish being collected immediately before spawning, while others were collected immediately after spawning.

The mean diameter of mature ova from *Etheostoma fonticola* was not positively correlated with total length of the fish. In fact, the smallest mature female (24.4 mm total length) had 18 mature ova with a mean diam of 1.17 mm. This was greater than the mean diam of mature ova found in all sizes of mature females (1.10 mm). This agrees with the findings of Hubbs *et al.* (1968) concerning *E. lepidum* and *E. spectabile*. In contrast, Hoar (1957) reported that the final size of the ova of fishes depends both on the size of the parent and her level of nutrition during the period preceding spawning. Casual observations indicated that there was a large available food supply for all sizes of *E. fonticola* in the study area.

It has been stated that fishes which provide parental care to the ova spawn fewer ova than those that do not (Allee *et al.*, 1949; Hoar, 1957; Bennett, 1970; Lagler *et al.*, 1962; Royce, 1972). This generalization apparently does not apply to darters since many provide little or no parental care and also spawn few ova (Hubbs *et al.*, 1968; Reeves, 1907; Scalet, 1973; Williams, 1959). *Etheostoma fonticola* provides no parental care to the ova (Strawn, 1955) and has very low fecundity. Williams (1959) concluded that evolutionary development of parental care does not entail a reduction in fecundity, but other factors such as available space in the body cavity are limiting. In addition, Hubbs and Strawn (1957b) stated that water temperature affected fecundity of *E. lepidum*. Thus, it appears that fecundity of darters is controlled by a variety of genetic and environmental factors.

Sexual dimorphism.—Sexual dimorphism, both slight and extreme, is exhibited by darters (Fahy, 1954; Gosline, 1947; Lachner *et al.*, 1950; Lake, 1936; Petravicz, 1936; Petravicz, 1938; Reeves, 1907; Reighard, 1913).

Etheostoma fonticola exhibits sexual dimorphism in four morphological characters. First, the bodies of males have a more intense light and dark vertical banding pattern than those of females. Second, the coloration of the males' first dorsal fin is divided into five distinct bands which are black, clear, red, clear and black. This banding pattern may also occur in larger females but is not as conspicuous as in the males. Third, the genital papillae of males distinctly differ in both shape and size from those of females. Females possess papillae which are rather long, fleshy and forked, while the papillae of males are shorter, not as fleshy, and pointed rather than forked. This dimorphic character is visible in all but the very smallest fish. Fourth, the pelvic fins of males have nuptial tubercles and are bulkier and more fleshy than those of females.

Sex ratio.—Sex determinations of *Etheostoma fonticola* (325 males and 234 females) revealed a sex ratio of 1.39:1.00. A chi-square test for two independent samples (Siegel, 1956) showed this sex ratio was significantly different (α = 0.05; 1 df) from a 1:1 ratio.

Sex ratios vary among darter species. *Etheostoma gracile, E. blennioides, Percina sciera* and *E. coeruleum* have 1:1 sex ratios (Braasch and Smith, 1967; Fahy, 1954; Page and Smith, 1970; Reeves, 1907); *E. flabellare, E. squamiceps* and *E. olmstedi* have more females than males (Lake, 1936; Page, 1974; Tsai, 1972); and *E. zonalis, P. phoxocephala,* and *E. maculatum* have more males than females (Lachner *et al.,* 1950; Page and Smith, 1971, Raney and Lachner, 1939).

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