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ILLINOIS NATURAL
HISTORY SURVEY

THE LIFE HISTORY OF THE CYPRESS DARTER, Etheostoma proeliare, IN MAX CREEK, ILLINOIS

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Biological Notes No. 106

Illinois Natural History Survey
Urbana, Illinois - July 1978

State of Illinois
Department of Registration and Education
Natural History Survey Division

Fig. 1.—The distribution of *Etheostoma proeliare*. The solid black line represents the Coastal Plain boundary. The study area is enclosed within the circle.

THE LIFE HISTORY OF THE CYPRESS DARTER, *ETHEOSTOMA PROELIARE*, IN MAX CREEK, ILLINOIS

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Of the three species (*Etheostoma proeliare*, *E. fonticola*, *E. microperca*) in the subgenus *Microperca*, *E. proeliare* has been the poorest known ecologically. This report provides information on the life history of *E. proeliare* at a study site on Max Creek, Johnson County, Illinois. A similar report being completed on *E. microperca* will compare information on *E. microperca* and *E. proeliare* with that recently published on *E. fonticola* (Schenck & Whiteside 1976, 1977a, 1977b).

Etheostoma proeliare was described by Hay (1881) from a specimen collected in a tributary of Tusculum River at Corinth, Alcorn County, Mississippi. The species ranges from southern Illinois and southeastern Missouri south to Texas and the Florida panhandle. In general the distribution of the species is limited to streams and lakes on the Coastal Plain (Fig. 1). A detailed morphological description of the species is found in Burr (1978).

We are indebted to John A. Boyd, Patti A. Burr, Michael A. Morris, Craig W. Ronto, Timothy E. Vogt, and Donald W. Webb for aid in collecting specimens; to Edward A. Lisowski, John K. Bousman, and Donald W. Webb, all of the Illinois Natural History Survey, for identification of stomach contents; David F. Oettinger and William L. Current, University of Nebraska-Lincoln, for identification of parasites; and to Philip W. Smith, Illinois Natural History Survey, for counsel and advice.

We are grateful to the following curators and their institutions (abbreviations used in text and Table 2) for granting specimen loans, laboratory space, and other courtesies: Anthony A. Echelle, Baylor University (BU); Eugene C. Beckham, formerly at Cornell University (CU); Robert K. Johnson, Field Museum of Natural History (FMNH); Ralph W. Yerger, Florida State University (FSU); Henry W. Robison (HWR), Southern Arkansas University; Illinois Natural History Survey (INHS); F. B. Cross, University of Kansas (KU); Glenn H. Clemmer, Mississippi State University (MSU); Neil H. Douglas, Northeast Louisiana University (NLU); Rudolph J. Miller, Oklahoma State University (OAM); Loren G. Hill, University of Oklahoma (OUMZ); John D. McEachran, Texas A & M University (TCWC); Thomas M. Buchanan (TMB).

This paper is published by authority of the State of Illinois, IRS Ch. 127, Par. 58.12, and is a contribution from the Section of Faunistic Surveys and Insect Identification of the Illinois Natural History Survey. Dr. Brooks M. Burr, formerly a Research Assistant at the Survey, is Assistant Professor, Department of Zoology, Southern Illinois University, Carbondale. Dr. Lawrence M. Page is an Associate Taxonomist at the Survey.

Westark Community College; Robert F. Martin, University of Texas Natural History Collection (TNHC); Royal D. Suttkus and Eugene C. Beckham, Tulane University (TU); Herbert T. Boschung, University of Alabama Ichthyological Collection (UAIC); Reeve M. Bailey and Robert R. Miller, University of Michigan Museum of Zoology (UMMZ); Victor G. Springer, National Museum of Natural History (USNM); and David A. Etnier, University of Tennessee (UT).

This study was supported primarily by a grant from the USDA Soil Conservation Service and National Science Foundation grant DEB 76-22387. The illustrations were prepared by Illinois Natural History Survey Illustrators Lloyd LeMere and Craig W. Ronto and Survey Photographer Larry Farlow. The cover illustration is from a drawing by Alice A. Prickett. The manuscript was typed by Alice K. Adams and edited by Shirley McClellan, Assistant Technical Editor. Leslie W. Knapp, National Museum of Natural History, served as guest reviewer.

STUDY AREA

Etheostoma proeliare is distributed sporadically in southern Illinois and is common only in highly localized areas. Max Creek in Johnson County is a tributary of Bay Creek (Ohio River drainage), and at the Illinois Route 147 bridge (4 km SW Simpson) and for a short distance downstream, *E. proeliare* is one of the most common fishes found. This site (Fig. 2) was selected for the life-history study.

Max Creek transects the Shawnee Hills and the study area lies in a deep valley. The substrate at the study area is mostly hard clay with some sand and patches of small gravel. Water is seldom over 1 m deep. Several springs enter Max Creek upstream from the study area. During high water the current is moderately fast and habitats are poorly defined. During low water clay-bottom pools and gravel-bottom riffles are formed. Filamentous algae are abundant in summer and fall in both riffles and shallow pools that are exposed to sunlight, but are absent in winter and early spring and in deep pools and shaded areas. Some rooted vegetation is present in shallow water areas. During the low water levels in late fall and winter, a layer of leaves and sticks covers the bottom of the stream. The accumulations of leaves and sticks are eventually washed away but remain, mostly along pool margins, well into the summer.

Fig. 2.—Max Creek at Illinois Route 147 bridge, 4 km SW of Simpson, Johnson County, Illinois. In the top photo, taken on 15 September 1976, the creek is low with much exposed vegetation. In the bottom photo, taken on 4 May 1977, the creek is high and roiled.

Fifty species of fishes occur in the Bay Creek system. At the study area the most common, in addition to *E. proeliare*, are *Pimephales notatus*, *Notropis fumeus*, *N. unbratilis*, *Cottus carolinae*, *Aphredoderus sayanus*, *Etheostoma chlorosomum*, *E. gracile*, *Fundulus olivaceus*, and *Erimyzon oblongus*. Other darters in the Bay Creek system are *Percina maculata*, *Etheostoma caeruleum*, *E. kennicotti*, *E. nigrum*, and *E. spectabile*.

METHODS

Methods of study were the same as those employed by Page (1974:4-5) except as noted below. Observations and minnow-seine collections were made at approximately monthly intervals from 25 October 1975 to 9 October 1976. A total of 482 specimens was preserved and stored in 10-percent formalin. Additional data on reproduction were accumulated on 4 May 1977.

Attempts were made to collect specimens by habitat, but often boundaries of habitats (e.g., pools, riffles) in Max Creek were poorly defined. When it became evident that *E. proeliare* was found wherever dead leaves, sticks, and other debris were accumulated or vegetation was growing, regardless of habitat, these attempts were discontinued.

In addition to specimens from the study area, *E. proeliare* from nearly all museum collections were examined to determine probable spawning periods in other localities and other years. Indicators of spawning preparedness were the following: maximally tuberculate males, well-developed lateral pelvic fin flaps on males, peak breeding coloration, and females swollen with mature ova (often visible through body wall). Collections of specimens were considered to be in spawning condition if all, or if only some of the specimens, were in peak reproductive condition.

HABITAT

In the study area the greatest concentrations of *E. proeliare* were in accumulations of leaves and sticks on the bottom of the stream and, secondarily, in filamentous algae. Pools, more than riffles, acted as depositories for leaves and sticks, and generally yielded more specimens of *E. proeliare* than did riffles. It was clearly the presence of leaves and/or vegetation that was important to *E. proeliare* rather than the physical attributes of pools and riffles; pools and riffles without leaves or vegetation yielded few or no *E. proeliare*. Pools and riffles with leaves or vegetation typically yielded large numbers of *E. proeliare*.

Collections of *E. proeliare* made elsewhere (in Alabama, Illinois, Kentucky, Louisiana, and Missouri) by the authors support their observation at the study area of the affinity of the species for leaves and vegetation. In some streams in which *E. proeliare* is found, the vegetation inhabited is nothing more than exposed tree roots along bank undercuts. Both

streams and lakes are inhabited by *E. proeliare* and, in general, the more leaves or vegetation present, the larger the population of *E. proeliare*.

The preferred habitat of *E. proeliare* is best described as leaf-laden and/or vegetated sluggish water bodies, including small to large streams and the margins of lakes. No distinction between the habitat of young *E. proeliare* and that of adult *E. proeliare* is evident.

REPRODUCTION

Reproductive Cycle of the Male

The enlargement of the genital papilla of the male is a gradual process, occurring over many months

Fig. 3.—Genital papillae of *Etheostoma proeliare*. A, non-breeding male; B, breeding male; C, nonbreeding female; D, breeding female. The breeding specimens were 1 year old, collected on 13 April 1976; the nonbreeding specimens were —1 year old, collected on 15 September 1976.

rather than only during the immediate prespawning period. By March the papilla is proportionally much larger than those of males collected earlier in their life history (Fig 3). The testes of breeding males are greatly enlarged, white and spongy. Those of non-breeding males are small and translucent.

In studies of other darters it was possible to recognize a minimum length that males had to attain to become sexually mature and spawn their first year. In *E. proeliare* all spring-collected males, including the smallest, a 25.5-mm male collected in April, were sexually mature and apparently capable of spawning.

As early as late January males began to develop breeding colors and structures. The first dorsal fin of the male began to develop more black pigment in the basal one-third of the anterior membranes and the lateral flaps of skin began to form on the pelvic fins. No tubercles were present on January-collected specimens, and the anal and pelvic fins had only a few scattered melanophores.

By late February tubercles were developed sparsely on one or two anal rays and slightly better developed on the median pelvic rays of a few large males. The first dorsal fin pattern intensified, the pelvic fin flaps

Fig. 4.—Breeding male (upper) and breeding female (lower) *Etheostoma proeliare* collected in Max Creek on 10 March 1976. The male was 33 mm; the female was 31 mm. Drawings by Alice A. Prickett.

were nearly developed to their maximum, and the anal and pelvic fins had a heavy concentration of melanophores.

From about the second week of March to the third week of June, the male breeding colors and structures were at their peak development (Fig. 4). The body was dark brown with 8–10 intense mid-lateral blotches interspersed with specks of iridescent cream-yellow. The teardrop and postorbital bar were intense black. The base of the pectoral fin and the bottom half of the opercle were iridescent cream-yellow. The flesh overlying the back of the head, second dorsal, and caudal fins was thick and milky white. The iris of the eye was bright red-orange with some iridescent green. The first dorsal fin was black on the basal one-third of the anterior membranes, more gray in the posterior membranes. Medially, the anterior membranes of the first dorsal fin had intense red-orange spots; similar spots were more subdued in the posterior membranes. The second dorsal and caudal fins had five or six amber-orange bands. The anal and pelvic fins had heavy concentrations of melanophores, mostly basally on the membranes. The pectoral fin rays were sharply outlined by melanophores.

Tubercles were developed maximally on all the pelvic fin rays and all the anal fin elements except the second spine (when present), and were concentrated most heavily on the central portions of the fin rays. The lateral pelvic fin flaps were developed maximally with the skin greatly expanded on both sides of the pelvic spine and between pelvic rays one through three.

Reproductive Cycle of the Female

The genital papilla of the female enlarged over a several-month period, and by the spawning period was a swollen bilobed structure (Fig. 3) much different from the papilla of the male.

The female color and pattern change little prior to and during the breeding period (Fig. 4). Some females developed a suffusion of orange in the anterior portion of the first dorsal fin, an orange iris of the eye, and amber second dorsal and caudal fin bands. Other fins were clear generally except that the pectoral rays were often distinctly outlined by melanophores.

Fig. 5.—Mature eggs removed from an ovary of *Etheostoma proeliare*.

Small white ova were discernible in females collected as early as November. Somewhat larger, yellow ova appeared in females as early as January, and larger dark yellow ova were found in females collected as early as March. Prior to spawning the large dark yellow ova transformed into translucent, half-doughnut shaped eggs with one large oil droplet (Fig. 5). Eggs averaged 0.7 mm across.

All females collected in spring (March to June) had large, maturing or translucent ova and apparently would have spawned. The smallest spring-collected female was 25.8 mm and was collected on 4 May 1977.

In 17 females collected in March–June 1976 and in May 1977 the number of mature ova ranged from 26 to 116 (Table 1). For these females there was no significant correlation between the number of mature ova and the standard length, nor between the number of mature ova and the adjusted body weight; for both relationships the correlation coefficient (r) was less than 0.10. Significant correlations were found for these relationships in other species of darters, and the absence of correlation for the number of mature ova and size of *E. proeliare* may be because they spawn only once (at 1 year of age) and are all about the

TABLE 1.—Relationship between size, age, and ovary weight of *Etheostoma proeliare* females and the number of mature ova produced. All females were 1 year (11–14 months) old.

Standard Length in mm	Adjusted Body Weight in Grams ^a	Month of Collection	Ovary Weight in Grams	Number of Mature (Dark Yellow or Translucent) Ova
28	0.27	March	0.06	44
29	0.29	April	0.09	98
30	0.36	April	0.09	72
30	0.39	April	0.10	116
31	0.39	April	0.08	112
32	0.44	April	0.08	26
32	0.46	April	0.09	90
29	0.26	May	0.06	56
29	0.27	May	0.06	58
30	0.37	May	0.05	78
31	0.37	May	0.07	90
31	0.38	May	0.06	110
31	0.40	May	0.09	106
33	0.44	May	0.07	76
35	0.47	May	0.09	98
36	0.51	May	0.09	92
30	0.34	June	0.02	28

^a Adjusted body weight is the specimen's weight after removal of the ovaries, stomach, intestine, and liver.

same size at spawning. Another reason may be that *E. proeliare* disperses its eggs over a sizeable area rather than concentrates them as some other species of darters (especially species of *Catnotus*) do. Spawning is more likely to be interrupted and some of the 17 females examined may have laid a portion of their eggs prior to being captured; if so, egg counts made on them were not of the total number of eggs produced.

From September until the spawning season, ovaries increased markedly in size in relation to the body of the female (Fig. 6). For the females examined, the relationship between the mean of the weight of the ovaries divided by the adjusted body weight (Y) and the month (X), with September = 1 and April (the month of the greatest spawning activity) = 8, was $\log Y = 0.848 + 0.202 X$, with $r = 0.909$ (Fig. 6). The proportionally largest ovaries (equaling 31 percent of the adjusted body weight) were found in a 29-mm female collected on 13 April 1976. In the 17 females represented in Table 1, ovary-weight-to-adjusted-body-weight ratios ranged from 0.059 to 0.310 and averaged 0.194.

Spawning

At the study area *E. proeliare* was ripe from March to June. Some individuals transferred from Max Creek to aquaria on 10 March 1976, 13 April 1976, 29 April 1976, and 4 May 1977, spawned on the following day and for a few days thereafter. The stream temperatures at the time of capture of ripe *E. proeliare* ranged from 9.5° to 16°C; aquaria tem-

Fig. 6.—Monthly variations in ovarian weight relative to adjusted body weight of 5- to 14-month-old *Etheostoma proeliare*. The vertical axis is a logarithmic scale.

peratures ranged from 22° to 25°C. The sudden rise in temperature may have caused spawning to occur earlier among captive individuals than among those remaining in Max Creek. Spawning was not observed in Max Creek, but the spawning season there, based on tank observations and preserved individuals, is approximately from mid-March to early June. Ripe individuals were captured in shallow, sluggish water with accumulations of dead leaves, algae, or other vegetation, and this is probably the spawning habitat.

Examinations of preserved museum specimens from throughout the range of the species indicated that spawning occurs earlier in the southern portions of the range and later in northern portions (Table 2). Specimens from Lake Pontchartrain drainages are ripe from January through April. Most of the more northern populations are ripe from March to June. One collection from the upper St. Francis River, Missouri, (KU 9276) had both males and females in extreme spawning condition on 2 August. The geographic variation in spawning periods is related presumably to the warmer water temperatures on earlier dates at more southern latitudes.

Spawns in aquaria occurred in early morning, during midday, and in the evening, and were observed many times. Courting consisted mainly of a

TABLE 2.—Frequency distribution by month of collection of breeding *Etheostoma procliare* from throughout the range of the species. Drainages are arranged primarily by latitude and geographic propinquity where possible. Numbers in parentheses are numbers of collections supporting a reproductive condition, as explained under Methods. Museum collection abbreviations are given in the introduction.

Drainages	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Collection Dates
Lake Pontchartrain, LA (10—BU 234, 306; CU 15535; NLU 977, 1662, 4142; TU 45041, 75882, 83129; UMMZ 16117)	4	1	3	2	..	..	..	..	4 January–8 April
Mermentau-Calcasieu R., LA (2—TU 44565, 50225)	..	1	1	..	..	..	..	..	8 February–23 March
Trinity R., TX (2—TCWC 4025.4; TNHC 1348)	..	..	2	..	..	..	..	..	23–24 March
Red R., LA, TX, OK, AR (12—BU 213, HWR 72-11; OAM 5054, 5629, 6464; OUMZ 37979; TCWC 4064.7, 4068.8; TNHC 522; TU 93010; USNM 163116, 172985)	..	1	4	6	1	..	..	..	17 February–18 May
Ouachita R., LA, AR (19—BU 1561; HWR 72-12; INHS 75701; NLU 1414, 15185, 31205, 31277, 31368, 31480, 31671, 33188, 33302, 33360; TCWC 129.18; TMB 74-16; TU 76118, 87611; USNM 165951, 172567)	..	6	5	7	1	..	..	..	4 February–10 May
Big Black-Yazoo R., MS (7—FSU 10554; NLU 161110; UMMZ 144699, 161062, 161110, 161136; USNM 165959)	..	..	1	6	..	..	..	..	1 March–21 April
Upper Pearl R., MS (4—CU 37538; FSU 10643, 10676; TU 39989)	..	..	1	3	..	..	..	..	10 March–24 April
Tombigbee-Black Warrior R., AL (10—CU 64665; TU 40499, 76978, 77045; UAIC 915, 1296, 1865, 1892, 1898, 4507.08)	..	2	4	4	..	..	..	..	4 February–22 April
Arkansas R., AR (8—KU 6191, 6208, 9826; OAM 4549; TMB 74-15; TU 2224; UMMZ 177142; USNM 165891)	..	1	1	6	..	..	..	..	16 February–22 April
White R., AR (4—FSU 14498; TMB 72-3; TU 49830, 49970)	..	..	1	2	..	1	..	..	26 March–6 June
Hatchie R., MS, TN (2—MSU 2670, 6058)	..	..	..	1	1	..	..	..	8 April–6 May
Tributaries, Tennessee R., MS, TN (2—TU 87969; UT 91.1063)	..	..	1	..	1	..	..	..	1 March–8 May
St. Francis R., AR, MO (4—FMNH 60731; FSU 14342; KU 9276, 16079)	..	..	1	..	..	2	..	1	11 March–2 August
Tributaries, Ohio R., IL, KY (7—INHS 1358, 75840; Max Creek specimens)	..	..	3	2	1	1	..	..	3 March–17 June

male and female darting about the aquarium with the female leading the male close behind her. At times the male mounted the female, clasped her upper sides with his large pelvic fins, and while mounted he occasionally rubbed his chin on the top of her head and on her cheeks in a way similar to the courting behavior described for *E. gracile* (Braasch & Smith 1967: 7).

The female selected the site for egg deposition and with the male close behind her elevated to the site (Fig. 7). Eggs ranged from 0.5–1.1 mm across and were attached to dead leaves, twigs, the sides and undersides of large rocks, and the glass sides of the aquarium. When the egg site was reached, the male mounted the back of the female; the two bodies vibrated together for a few seconds and were curved in such a way that the female genital papilla was placed on the selected spot where 1–3 adhesive eggs were laid. The male body was curved such that milt could be released near the eggs. At the instant of egg

laying the female always had her mouth wide open; the male's mouth was always closed. Eggs were laid as high as 13 cm above the substrate of the aquarium.

Typically, several eggs were laid at one site (e.g., underside of leaf). After 1–3 eggs were laid, the pair of darters dropped to the bottom and separated and rested for as long as a minute before they resumed spawning. Then the pair darted to a site 5–15 cm away from the first site and laid several more eggs. This sequence was repeated many times. Eggs were laid most often on dead leaves, and as many as 45 eggs were found on one leaf.

Laying eggs on leaves, undersides of rocks, etc., required that the spawning pair assume vertical and inverted positions. To maintain these positions, rapid vibrations of the caudal and pectoral fins were required. The male position on top of the female (even while inverted) was firmly maintained by the expanded male pelvic fins, which enabled him to tightly grip the middorsum of the female. The male

Fig. 7.—*Etheostoma proeliare* spawning in aquaria. Top: Male and female are inverted as egg and sperm are released on underside of leaf. Middle: Male and female in vertical position as egg and sperm are released on underside of leaf. Bottom: Male and female descending from egg deposition site. Note several eggs on edge of underside of leaf.

anal fin was always fully extended and pressed against the side of the female. The second dorsal fin of the female was pressed against the side of the male above his anal fin. The female first dorsal fin was retracted, but the male's dorsal fins remained fully spread. Some males which were observed spawning in aquaria on 10 March 1976 did not have the anal and pelvic fin tubercles developed. In this species the structures are not necessary for maintenance of body contact between the sexes, and are probably not used in defense; when present they may, however, aid in stimulation of the female as has been suggested for other fishes (see review by Wiley & Collette 1970: 148).

In aquaria females were not observed to spawn with more than one male, but in a natural environment, especially in a highly populated area, females may spawn with more than one male. When two males and five females were placed in an aquarium, both males successfully spawned, but the smaller male spawned more often and was observed to spawn with three different females. On several occasions the smaller male pursued and attempted to mount the larger male. Neither sex gave any attention to the eggs after spawning.

Other darters which spawn on live or dead vegetation similar to that utilized by *E. proeliare* (i.e., excluding riffle plants) are *E. microperca* (Petravicz 1936: 81–82; Winn 1958a: 201–202, 1958b: 161), *E. fonticola* (Strawn 1956: 14), *E. gracile* (Braasch & Smith 1967: 7), *E. fusiforme* (Fletcher 1957: 203; Smith 1907: 269), *E. exile* (Winn 1958a: 198, 1958b: 161), *E. edwini* (Williams 1976: 107), and *E. chlorosomum* (Winn 1958b: 189). The spawning of *E. proeliare*, in which the male clasps the back of the female with his pelvic fins and goes up into a vertical or inverted position, is most similar to that described for the closely related *E. microperca*. Detailed observations on the spawning act of the closely related *E. fonticola* have not been published, but Strawn's (1956: 14) brief description indicates a similar behavior.

Sexual Dimorphism

A taxonomic study of *E. proeliare* from throughout the range of the species revealed that 7 of 16 morphometric characters measured on breeding specimens showed highly significant ($P < 0.005$) sexual dimorphism (Burr 1978). Males have significantly longer heads; longer postdorsal lengths; deeper caudal peduncles; and longer pelvic, pectoral, anal, and second dorsal fins. Sexual dimorphism in tuberculation, pelvic fin structure, coloration, and genital papillae are discussed elsewhere in this paper.

DEVELOPMENT AND GROWTH

Eggs incubated in aquaria at 10°C (50°F) developed to near hatching but failed to hatch. Eggs

Fig. 8.—*Etheostoma proeliare* hatchling (3.7 mm in total length).

incubated at 15°C (60°F) hatched in 300 ± 9 hours (12.5 days), at 20°C (67°–68°F) hatched in 211 ± 23 hours (8–10 days), and at 22°–23°C (71°–74°F) hatched in 131 ± 9 hours (5.5 days).

Hatchlings ranged from 3.4 to 3.7 mm in total length and were mostly translucent but had melanophores on the head, yolk sac, and some of the myomeres (Fig. 8). The pectoral fins and jaw were well developed as in other species of *Etheostoma* studied (e.g., *E. gracile*—Braasch & Smith 1967: 9; species of *Catnotus*—Page 1974: 11, 1975: 8–9; and Page & Burr 1976: 8).

On 17 June 1976 a series of 30 young *E. proeliare* ranging from 9 to 19 mm was collected in the study area. At 9 mm melanophores were loosely concentrated on top of the head, along the mid-side and at the fin bases. At 12 mm lateral blotches and dorsal saddles were discernible, and at 15 mm the color pattern of the adult had formed.

Scales were not present at 9 mm. At 12 mm squamation was nearly complete, but scales did not ap-

Fig. 9.—Size distribution by age of *Etheostoma proeliare* collected in Max Creek between 25 October 1975 and 9 October 1976. Black dots represent sample means for males; circles represent sample means for females. Regression line is for both sexes. A total of 482 specimens is represented.

pear on the cheeks, opercles, and prepectoral areas until considerably later (at about 20 mm on specimens collected 13 July 1976). Head canals began forming at about 12 mm and were completed between 15 and 17 mm. The lateral line began forming at about 14 mm.

Males and females grew at nearly the same decreasing rate (Fig. 9). The relationship between standard length (Y) and age in months (X) for males is $Y = 10.8 + 18.08 \log X$, with $r = 0.876$, and for females is $Y = 11.7 + 17.08 \log X$, with $r = 0.922$.

The largest specimen examined from Max Creek was a 36.4-mm male collected on 20 May 1976. The largest specimen known is a 39.6-mm female collected on 18 February 1977 from Cheniere Lake, Ouachita Parish, Louisiana.

At 1 year (12 months), males (N = 11) averaged 29.2 mm and females (N = 24) averaged 30.7 mm. *E. proeliare* reached one-half of the first year's mean growth in about 8 weeks. This is a shorter period than that recorded for other darters except *E. gracile* and *Percina phoxocephala* which were estimated to have reached one-half of the first year's mean growth in only 1 week (Braasch & Smith 1967: 9) and 2 weeks (Page & Smith 1971: 9), respectively.

DEMOGRAPHY

Density

Density samples were made by habitat on six separate dates but because habitat (e.g., pool, riffle) boundaries were defined poorly and the species occupied leaves and vegetation regardless of habitat, these data are not presented. The highest density found was 5.5 *E. proeliare*/m² in a vegetated, gravel area below a riffle on 21 January 1976.

Composition

Of the 482 *E. proeliare* collected in Max Creek between 25 October 1975 and 9 October 1976, 93.4 percent were up to 1 year of age and 6.6 percent were between 1 and 2 years of age (Table 3).

TABLE 3.—Distribution of sexes and year classes in samples of *Etheostoma proeliare* collected in Max Creek between 25 October 1975 and 9 October 1976.

Sex	Number by Year Class		Total
	-1	1+	
Male	222	6	228
Female	228	26	254
Total	450	32	482

There was no significant deviation from a 1 to 1 sex ratio in the first-year (-1) age class, but because of greater longevity females strongly predominated [4.3 to 1.0 ($\chi^2 = 12.5$; $P < 0.005$)] in the 1+ year class.

Survival

Of the 228 males collected 97.4 percent were up to 1 year of age and only 2.6 percent were over 1 year of age. Of the 254 females collected, 89.8 percent were up to 1 year of age and 10.2 percent were over 1 year of age. Assuming that each year class was collected in proportion to its relative number in the population, only 2.7 percent of the first-year males and 11.4 percent of the first-year females survived to a second year. For males and females combined, the survival to a second year was 7.1 percent. These survival values are much lower than those for other darters studied, and the short life span of *E. proeliare* is a distinctive feature among darters. The oldest *E. proeliare* from Max Creek examined (assuming an April hatching) were one 18-month-old female collected October 1975 and two 18-month-old females collected in October 1976. The oldest male from Max Creek examined was a 15-month-old specimen collected in July 1976.

Migration

E. proeliare was found with relative ease at the study area during every month of the study period and there was no indication of any migration up and down the stream or from one habitat to another.

Territoriality

No territoriality was observed in *E. proeliare*, including among males before and during the breeding season. Petravicz (1936) did not observe territorial behavior in the closely related *E. microperca*, but later studies by Winn (1958b) showed that the species exhibited some territoriality. Winn suggested that overcrowding aquaria with too many individuals resulted in abnormal behavior; it is possible that aquaria used in this study were overcrowded and territoriality was inhibited. Perhaps under more natural conditions *E. proeliare* uses plants in the delimitation of a territory as was found for *E. microperca* (Winn 1958b: 168). If *E. proeliare* does not exhibit territorial behavior, it may be a response to the fact that the eggs are scattered over a loosely defined area and not in a small concentrated area selected and guarded by the male.

DIET

The stomach contents of 118 *E. proeliare* were mostly chironomid larvae and small crustaceans (Table 4). Insects other than chironomids made only small contributions to the diet. Compared to other darters studied, e.g., *Percina sciera* (Page & Smith 1970), *P. phoxocephala* (Page & Smith 1971), *P. nigrofasciata* (Mathur 1973), *Etheostoma squamiceps* (Page 1974), *E. kennicotti* (Page 1975), and *E. smithi* (Page & Burr 1976), *E. proeliare* fed more heavily on small crustaceans and less heavily on insects other than chironomids. This is probably a

TABLE 4.—Stomach contents of *Etheostoma proeliare* from Max Creek, by size class of darter. Figures in parentheses are numbers of stomachs examined.

Food Organism	Percent of Stomachs in Which Food Organism Occurred				Mean Number of Food Organisms per Stomach			
	<21 mm	21–25 mm	26–30 mm	>30 mm	<21 mm	21–25 mm	26–30 mm	>30 mm
	(19)	(23)	(53)	(23)	(19)	(23)	(53)	(23)
Arachnida								
Acarina	5.3				0.05			
Crustacea								
Cladocera	21.1	56.5	37.0	34.8	0.21	3.00	6.31	0.96
Ostracoda		8.7	3.7	8.7		0.13	0.04	0.09
Copepoda	73.7	87.0	79.6	82.6	2.53	8.56	12.22	5.65
Isopoda								
Asellidae								
<i>Asellus</i>	5.3	4.4	1.9	34.8	0.05	0.04	0.02	0.83
<i>Lirceus</i>			1.9	13.0			0.02	0.13
Amphipoda								
Hyalellidae								
<i>Hyaella</i>		17.4	22.2	13.0		0.35	0.56	0.22
Chilopoda			1.9				0.02	
Insecta								
Collembola								
Sminthuridae			3.7	4.3			0.04	0.04
Isotomidae			1.9				0.04	
Ephemeroptera		4.3	11.1			0.04	0.13	
Hemiptera								
Corixidae	5.3	4.3	1.9		0.11	0.04	0.02	
Diptera								
Tipulidae		4.3				0.04		
Chaooridae	5.3	8.7			0.05	0.13		
Chironomidae	100.0	69.6	75.9	95.7	8.05	4.35	3.87	22.13

function of the small body and mouth of *E. proeliare*, which makes ingestion of large insects (e.g., caddisflies and stoneflies) difficult, and also of the habitat in which *E. proeliare* lives. Small crustaceans are common in vegetation; insects such as mayflies, caddisflies, and stoneflies are much more common in rocky habitats.

As in most darters studied, chironomid larvae were an extremely important food item to *E. proeliare* of all sizes. Small crustaceans, especially copepods and cladocerans, were also important to *E. proeliare* of all sizes. In other darters (those cited above) small crustaceans were important to small individuals, but decreasingly so with an increase in the size of the darter. Isopods were consumed in significant amounts only by *E. proeliare* over 30 mm in standard length.

Chironomids and copepods were important diet items every month of the year (Table 5). Cladocerans were most important in the fall, isopods from March to September, and amphipods from May to December.

Rice (1942: 8–9) examined the stomach contents of 20 specimens of *E. proeliare* from Reelfoot Lake near Samburg, Tennessee. She found that mayflies made up 50 percent of the diet, copepods 35 percent, ostracods 10 percent, mosquito larvae 3 percent and leafhoppers 2 percent. No leafhoppers were found in the stomachs of Max Creek specimens, but springtails were present. The presence of leafhoppers and springtails indicates possible surface feeding by *E. proeliare* since both of these insect groups are terrestrial and would become submerged only accidentally.

INTERACTIONS WITH OTHER ORGANISMS

Competition

Other than *E. proeliare* the only darters regularly encountered at the study area were *E. chlorosomum* and *E. gracile*. *E. gracile* was usually in the vegetated areas most heavily occupied by *E. proeliare* but was much less common. *E. chlorosomum* was in deeper, clay-bottom pools. All three of these species lay their eggs on vegetation, but there is no evidence of competition for spawning sites in Max Creek where there is an abundance of dead leaves and vegetation in the spring.

The restricted distribution of *E. proeliare* in southern Illinois is difficult to understand. Many apparently suitable habitats in southern Illinois are uninhabited by *E. proeliare*. *E. gracile* and *E. chlorosomum* are much more widespread and common.

Predation

As potential predators of *E. proeliare*, 7 *Esox americanus* (84–155 mm), 1 *Noturus gyrinus* (84 mm), 4 *Aphredoderus sayanus* (35–66 mm), 1 *Centrarchus macropterus* (95 mm), 1 *Micropterus salmoides* (70 mm), 5 *Lepomis cyanellus* (75–129 mm), 4 *L. macrochirus* (56–95 mm), 2 *L. megalotis* (50–56 mm), and 1 *Cottus caroliniae* (68 mm) were preserved and later examined. The only ingested fish found were 2 *Aphredoderus sayanus* in the stomachs of 2 *Esox americanus*.

Parasitism

Of the 118 *E. proeliare* from which stomach contents were examined, two each contained one par-

TABLE 5.—Stomach contents of *Etheostoma proeliare* from Max Creek, by month of collection. Figures in parentheses are numbers of stomachs examined.

Food Organism	Percent of Stomachs in Which Food Organism Occurred												Mean Number of Food Organisms Per Stomach											
	Jan. (8)	Feb. (8)	Mar. (7)	Apr. (8)	May (10)	June (10)	July (13)	Aug. (10)	Sept. (10)	Oct. (18)	Nov. (8)	Dec. (8)	Jan. (8)	Feb. (8)	Mar. (7)	Apr. (8)	May (10)	June (10)	July (13)	Aug. (10)	Sept. (10)	Oct. (18)	Nov. (8)	Dec. (8)
Arachnida	...	...	...	...	...	10.0	...	...	...	...	...	...	...	...	...	...	...	0.10	...	...	...	...	...	...
Acarina	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Crustacea	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Cladocera	...	25.0	...	37.5	...	50.0	...	30.0	90.0	83.3	75.0	25.0	...	0.25	...	0.38	...	0.50	...	0.30	27.90	7.06	1.63	0.50
Ostracoda	...	...	...	...	...	10.0	...	...	10.0	22.2	...	...	...	...	...	...	...	0.10	...	...	0.10	0.28	...	...
Copepoda	100.0	87.5	71.4	75.0	70.0	70.0	46.2	80.0	100.0	88.9	100.0	100.0	19.75	28.75	5.00	4.38	3.90	3.00	1.31	2.10	6.10	5.33	8.38	30.75
Isopoda	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Asellidae	...	...	14.3	37.5	10.0	40.0	7.7	...	10.0	...	...	...	...	...	0.14	0.63	0.10	1.30	0.08	...	0.10	...	...	...
Lirceus	...	...	...	37.5	10.0	...	...	...	...	...	...	...	...	...	...	0.38	0.10	...	...	...	...	...	...	...
Amphipoda	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Hyalellidae	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Hyalella	...	...	...	...	10.0	20.0	7.7	10.0	50.0	38.9	12.5	12.5	...	...	...	...	0.10	0.50	0.08	0.10	1.10	1.22	0.13	0.13
Chilopoda	...	...	...	...	...	...	...	...	...	...	...	12.5	...	...	...	...	...	...	...	...	...	...	...	...
Insecta	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Collembola	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Sminthuridae	...	25.0	14.3	...	...	...	...	...	...	...	...	...	...	...	0.25	0.14	...	...	...	...	...	...	...	...
Isotomidae	12.5	...	...	...	...	...	...	...	...	...	...	...	0.25	...	...	...	...	...	...	...	...	...	...	...
Ephemeroptera	12.5	...	...	...	...	...	...	...	...	...	...	...	0.13	...	...	...	...	...	...	0.10	0.10	0.28	...	...
Hemiptera	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Corixidae	...	...	...	...	...	...	15.4	...	10.0	...	...	...	...	...	...	...	...	...	0.15	...	0.10	...	...	...
Diptera	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Tipulidae	...	...	...	...	...	...	...	...	10.0	...	...	...	...	...	...	...	...	...	...	...	0.10	...	...	...
Chaoboridae	...	...	...	...	...	...	23.1	...	...	...	...	...	...	...	...	...	...	...	0.31	...	...	...	...	...
Chironomidae	100.0	100.0	100.0	87.5	100.0	100.0	100.0	90.0	90.0	33.3	75.0	62.5	1.88	11.75	6.29	26.38	20.70	11.80	13.77	4.50	2.50	0.61	2.25	1.00

asitic nematode and two each contained one spiny-headed worm (*Acanthocephalus*). An unidentifiable tapeworm plerocercoid was found in a specimen collected 17 June 1976. The only external infestation was a protozoan parasite (*Myxosoma*) found on 8 specimens collected in May and June of 1976.

Specimens examined for external parasites from throughout the range of *E. proeliare* revealed infestation with a fluke [two collections—KU 15232 (Missouri); TCWC 4025.4 (Texas)] and a protozoan [four collections—CU 37538 (Mississippi); FSU 14342 (Arkansas); MSU 6058 (Tennessee); TCWC 4068.8 (Texas)]. A collection of *E. proeliare* from Amber Creek, Alexander County, Illinois (INHS 6042) made on 7 July 1964 contained specimens infected with a parasitic copepod (*Lernaea*).

Bangham & Venard (1942: 31) examined 15 specimens of *E. proeliare* from Reelfoot Lake, Ten-

nessee, for parasites. An acanthocephalan, *Leptorhynchoides thecatum*, was found in 9 of the 15 specimens; a digenetic trematode, *Neochasmus umbellus*, was found in 3 of the 15; and a nematode, *Contracaecum spiculigerum*, in 1 of the 15.

Hybridization

No natural darter hybrid combinations involving *E. proeliare* have been reported. Successful artificial crosses of *E. proeliare* have been made with the following species: *Ammocrypta vivax*, *Percina nigrofasciata*, *P. sciera*, and *E. stigmaeum* (Hubbs 1959) and *E. lepidum* and *E. spectabile* (Hubbs 1967).

SUMMARY

Life-history information on *E. proeliare* collected in Max Creek between 25 October 1975 and 9 October 1976 is summarized in Table 6.

TABLE 6.—Summary of life-history information on Max Creek *Etheostoma proeliare*.

Characteristic	Life-History Data
Principal habitat	Leaf-laden and/or vegetated, sluggish water bodies
Age at reaching sexual maturity	1 year
Age at first spawning	1 year
Size at reaching sexual maturity	All spring-collected individuals regardless of size were potential spawners
Sexual dimorphism	Adult males average smaller, have red-orange color in their first dorsal fins, develop expanded cup-like appendages on their pelvic fins and have longer heads, longer postdorsal lengths, deeper caudal peduncles, and longer pelvic, pectoral, anal and second dorsal fins
Breeding tubercles	Present on undersides of pelvic fins and both sides of anal fin in males only
Description of genital papillae	Females have a deeply forked, bilobed papilla; males have a pointed, tubular papilla
Number of mature ova in preserved females	26–116
Description of egg	0.7 mm across, translucent, adhesive and shaped like a half doughnut
Spawning period	From mid-March to early June
Spawning habitat	Relatively shallow, sluggish water with accumulations of dead leaves, filamentous algae, or other aquatic plants
Egg deposition sites	Dead leaves, twigs, sides of rocks, filamentous algae
Number of eggs laid per spawning act	1–3
Spawning position	Both male and female inverted or in vertical position, male mounted on back of female
Egg guarding	None observed; probably no parental care
Incubation period	131 ± 9 hours at 22°–23°C, 211 ± 23 hours at 20°C, 300 ± 9 hours at 15°C
Influence of sex on growth rate	Both sexes grew at approximately the same rate
Density	Up to 5.5 darters/m ² in vegetated areas
Sex ratio among young	1 male:1 female
Longevity	18 months
Maximum size	36.4 mm standard length
Migrations	None observed
Territoriality	None observed
Principal diet	Chironomid larvae and microcrustaceans

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