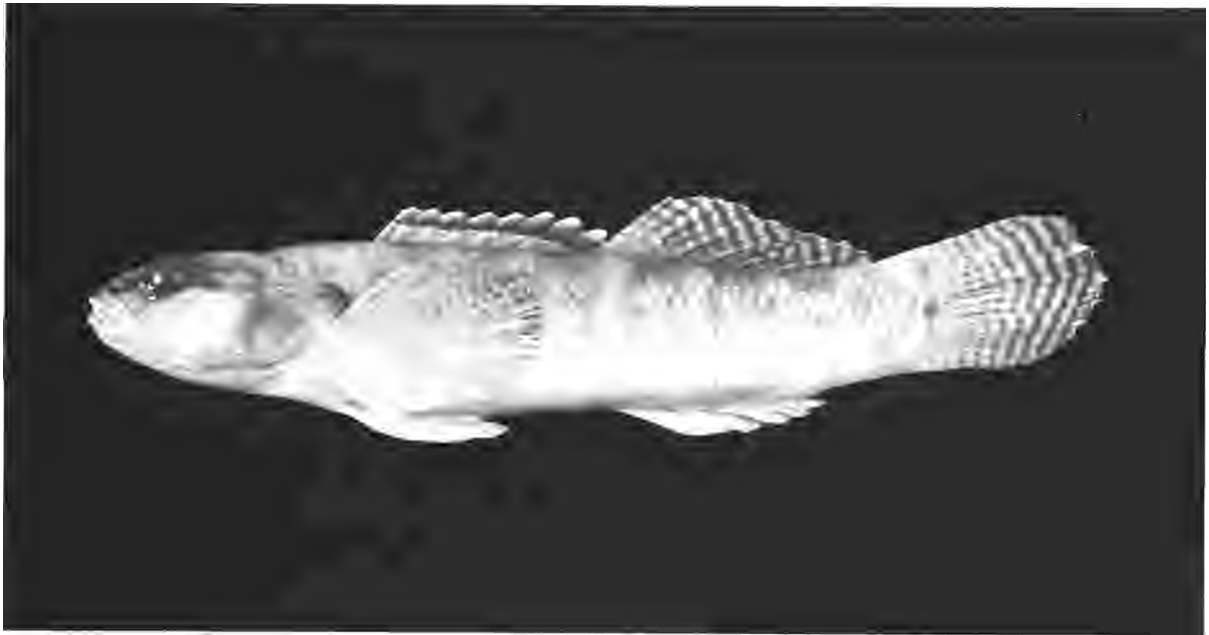


**THE LIFE HISTORY OF THE STRIPETAILED DARTER,
ETHEOSTOMA KENNICOTTI,
IN BIG CREEK, ILLINOIS**

Lawrence M. Page



ILLINOIS NATURAL HISTORY SURVEY

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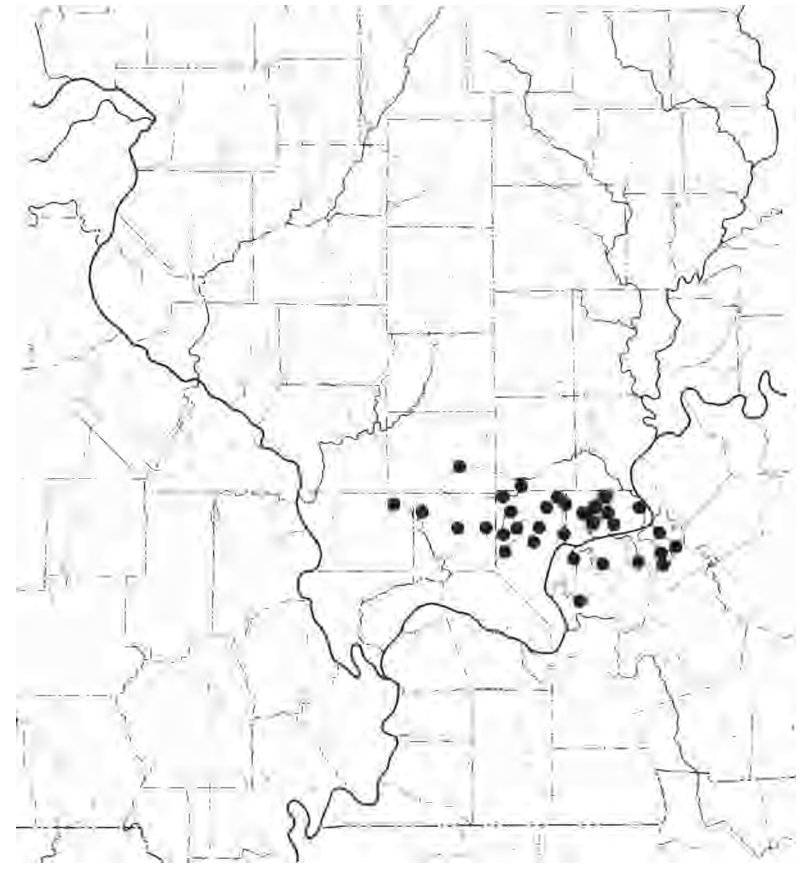
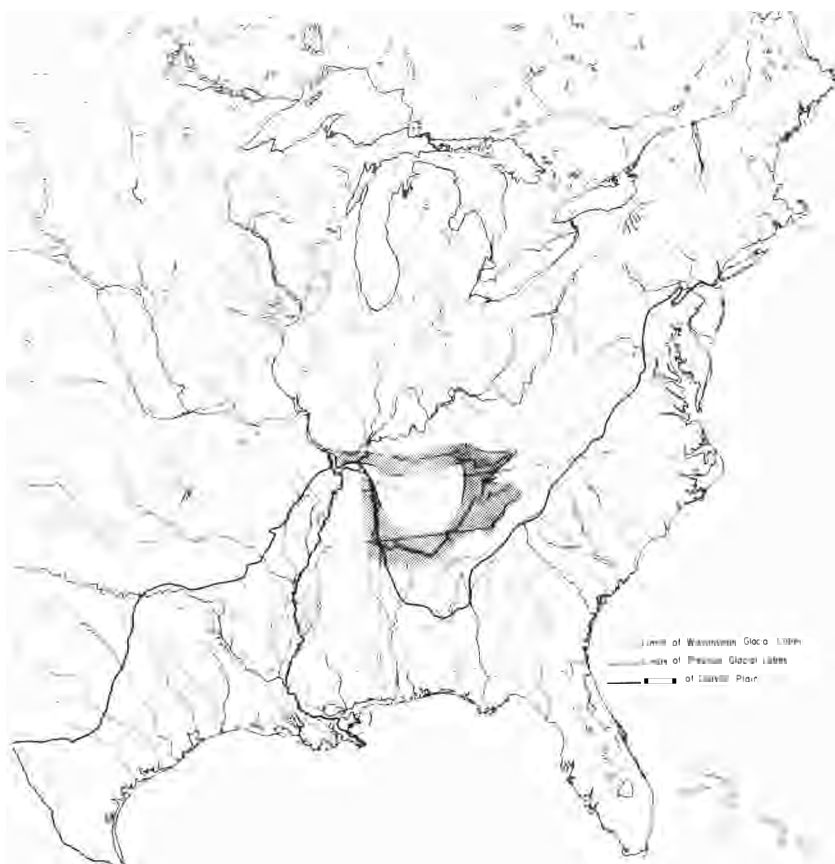


FIG. 1. — Distribution of *Etheostoma* (solid line). Wisconsin Glaciation (dotted line). Pleistocene Glaciation (solid line). of 1840s (line with square markers).

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THIS REPORT on the life history of *Etheostoma kennicotti* in Big Creek, Hardin County, Illinois, is the second of three reports on studies completed on species of the subgenus *Catonotus* in southeastern Illinois and the adjacent area of Kentucky between October 1970 and April 1974. The first report was on *E. squamiceps* (Page 1974); the third will be on *E. obeyense*.

E. kennicotti was described by Putnam (1863) from specimens collected by Robert Kennicott in "a rocky brook in Southern Illinois." The range of *E. kennicotti* (Fig. 1) includes the Ohio drainage of southern Illinois, tributaries of the Ohio River in a small area in extreme northwestern Kentucky, the Green River system in Kentucky and Tennessee, and Tennessee River tributaries in Tennessee, Alabama, Mississippi, and Georgia. Morphological descriptions of *E. kennicotti* are found in Putnam (1863:3), Jordan & Evermann (1896:1098), Forbes & Richardson (1908:311-312) — under the name *E. obeyense*, Moore (1968:150), and Collette & Knapp (1966:20-21).

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STUDY AREA, METHODS

The study area, Big Creek in Hardin County, Illinois (Fig. 1), was the same area in which *E. squamiceps* was studied (Page 1974) and is described by Lewis (1957) and Page (1974:3-4). Big Creek is a clear, spring-fed direct tributary of the Ohio

River with many gravel riffles, shallow slab rock pools, and deeper sand and gravel-bottom pools (hereafter referred to as non-slab pools).

The methods of study were the same as for *E. squamiceps* (Page 1974:4-5). The study of *E. kennicotti* began on 6 October 1970 and was terminated on 21 April 1974. A total of 1,380 specimens was preserved and examined. Unless stated otherwise, measurements in the text are standard lengths. For certain comparisons darters were divided into young (through 12 months) and adult (over 12 months) age groups.

HABITAT

Similar seining efforts in each of the three major habitats in Big Creek (gravel riffles, slab pools, and non-slab pools) each month during the study revealed a strong preference of adult *E. kennicotti* for slab pools (Table 1). Young *E. kennicotti* also usually preferred slab pools to riffles and non-slab pools but not as rigidly as adults, and at times were more common in the deeper non-slab pools. *E. kennicotti* were also most abundant in slab pools at other localities in Illinois, Kentucky, and Tennessee at which collections were made during the course of this study.

The preferred habitat of *E. kennicotti* is best described as the shallow, slab-rock-bottomed pools characteristic of upper elevation headwater streams (Fig. 2). The slab rocks are used for cover, and *E. kennicotti* were observed darting from beneath one rock to another, seldom remaining exposed for an extended period of time.

Although *E. kennicotti* and the closely related *E. squamiceps* share the strong association with slab stones, the preference of *E. kennicotti* for slab pools is in sharp contrast to the usual preference of *E. squamiceps* for slab riffles (Page 1974:6). In southern Illinois the 10 species most often found with *E. kennicotti* (in descending order of association, *Pimephales notatus*, *Semotilus atromaculatus*, *Fundulus olivaceus*, *Notropis chrysocephalus*, *Campeostoma anomalum*, *Lepomis megalotis*, *Notropis umbratilis*, *Etheostoma caeruleum*, *E. squamiceps*, *Erimyzon oblongus*) are those most successfully utilizing stream headwaters.

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TABLE 1. — Habitat distribution by percentages of *Etheostoma kennicotti* collected in Big Creek between 25 August 1971 and 19 June 1973.

Month	Number Collected	Percentages of <i>E. kennicotti</i> in		
		Slab Pools	Gravel Riffles	Non-slab Pools
Adults				
January	17	82	0	18
February	14	93	0	7
March	17	100	0	0
April	9	78	11	11
May	87	47	0	53
June	24	88	0	12
July	36	97	3	0
August	50	100	0	0
September	48	81	19	0
October	51	49	14	37
November	14	86	7	7
December	29	93	7	0
Young				
January	44	45	0	55
February	50	2	0	98
March	45	60	0	40
April	16	75	0	25
July	17	76	0	24
August	67	51	0	19
September	90	78	14	8
October	51	74	10	16
November	71	59	1	40
December	39	87	13	0

REPRODUCTION

Reproductive Cycle of the Male

As the spawning season approached, the genital papilla (Fig. 3) of the male enlarged, and, in contrast to the small and translucent testes of the nonbreeding male, the testes became large, white, and spongy. Breeding tubercles did not develop.

As in other darters, including other species of *Catnotus*, the color and intensity of the pattern of the male changed as the spawning season approached. The change was mainly an increase in melanization of the head similar to that described for *E. flabellare* (Lake 1936-818; Winn 1958b:172; Cross 1967:319) and the development of an orange-gold body color sharply contrasting with the white to light brown body of females and nonbreeding males.

The most extreme breeding pigmentation patterns were observed on spawning and nest-guarding males (Fig. 4 and 7). In contrast to females and nonbreeding males which have nearly identical pigment patterns, the body (especially the venter) was orange-gold in color, and the head, nape, and breast were darkened (although not nearly to the extreme of *E. squamiceps* breeding males). The orange knobs on the spines of the dorsal fin were swollen. The knobs and a thin, black submarginal band sharply contrasted with the unpigmented proximal portion of



Fig. 2. — Slab pool in the headwaters of Big Creek, Hardin County, Illinois.

the dorsal fin membrane. The pelvic fins, and in some males the anal fin, were milky white. The rays of the pectoral fins were outlined by rows of melanophores and were highly visible against the gold sides of the male. The gold iris of the eye appeared enlarged and especially prominent. The black vertical banding on the caudal and soft dorsal fins was much stronger and more visible than in nonbreeding individuals. The mottling on the sides of the body was partially obscured by variously devel-

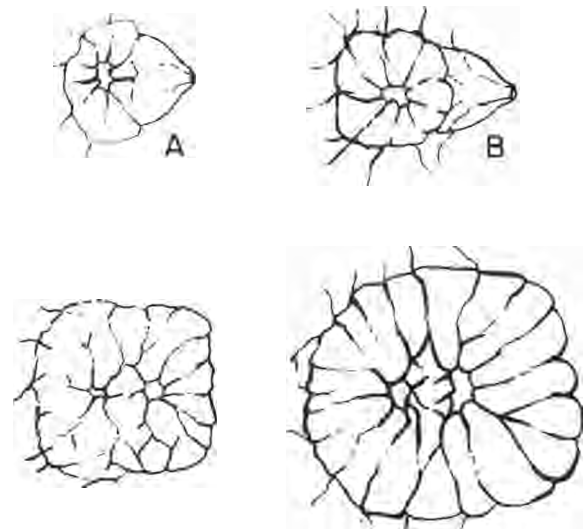


Fig. 3. — Genital papillae of *Etheostoma kennicotti*. A, nonbreeding male; B, breeding male; C, nonbreeding female; and D, breeding female. The nonbreeding specimens were 2+ years old, collected on 20 July 1971; the breeding specimens were also 2+ years old, collected on 16 May 1971.

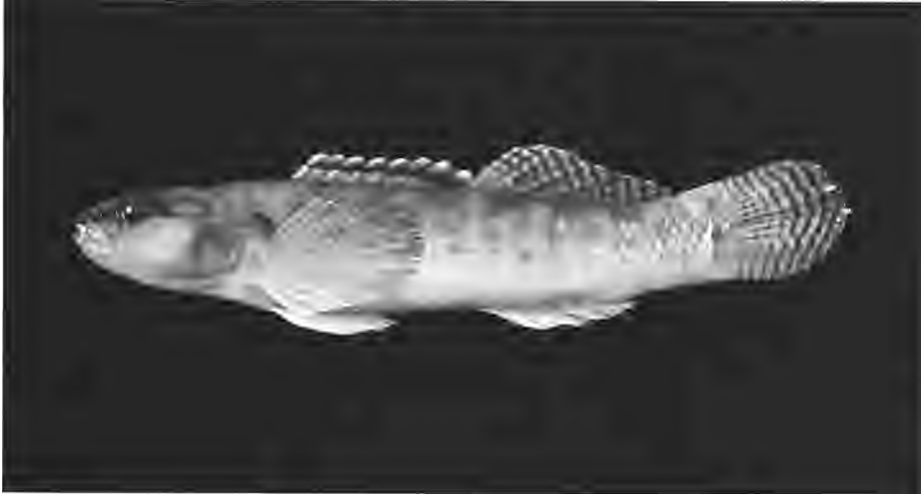


Fig. 4. -- Breeding male *Etheostoma kennicotti* 50.4 mm in standard length collected in Big Creek on 20 March 1974. Pigments have been somewhat subdued by preservation.

oped vertical banding, strong on some males and weak on others. The black humeral spot was prominent.

In larger breeding males the flesh of the head, and to a lesser extent that of the nape, becomes swollen. The swollen flesh may have a secretory function similar to that hypothesized for swollen flesh on *E. flabellare* by Cross (1967:320) or sensory and secretory functions similar to those discussed for the swelling of the head and nape of *Pimephales promelas* breeding males (Smith & Murphy 1974).

In March and April, males of *E. kennicotti* selected cavities under slab rocks as future nesting sites and defended them as breeding territories. The cavities were cleaned of silt and debris, mainly by vigorous tail-wagging motions as described for *E. squamiceps* (Page 1974:7).

Nesting territories of *E. kennicotti* in Big Creek were mostly established in the shallow (usually less than 30 cm), upstream slab pools also occupied heavily by *E. squamiceps*. In the spring the current in these pools was slight but sufficient to sweep most debris downstream. Less commonly, nesting territories were established among the concentrations of slab rocks at the margins of deeper pools. Deep water (over 40 cm) was usually avoided, and very rarely were *E. kennicotti* nests found in swift water.

In contrast to *E. squamiceps*, in which only the large males were found spawning, 1-year-old *E. kennicotti* as small as 35 mm were sexually mature and successful spawners. However, most nest territories found were held by large males, and large males presumably do most of the spawning.

Reproductive Cycle of the Female

As in other species of darters, generally the largest females of *E. kennicotti* developed mature ova earliest in the season. Females that were about 30 mm by 1 year of age developed mature ova and were capable

of spawning. A few females as small as 27 mm developed mature ova in late May but probably did not successfully spawn so late in the season.

Females did not undergo changes in coloration associated with the breeding season. The only marked morphological changes were the gross distention of the belly caused by maturing ova and the enlargement of the genital papilla (Fig. 3). Enlargement of the papilla began in most females by February or March; distention of the belly was apparent from only a few days to 2-3 weeks before spawning.

Small white ova began appearing in the females between September and December, appearing earliest in the largest individuals. A minimum size of approximately 20 mm was reached before white ova were discernible. Larger yellow ova were found as early as January in females 30 mm and larger, and appeared later in slower growing individuals. Large, maturing orange ova were present from March to May. Prior to spawning time, the mature ova became translucent.

The largest (and oldest) females produced the largest number of mature ova. In 17 ripe females collected in March, April, and May, the number of mature ova varied from 24 to 130 (Table 2). For these females the relationship between the number of mature ova (F) and adjusted body weight (W) was $F = 2.00 61.58W$, with $r = 0.631$, and between the number of mature ova and the standard length (L) was $\log F = -3.061 + 0.020 \log L$, with $r = 0.668$.

Estimates of the number of eggs laid in aquaria by five females (from 40 to 48 mm) were 20, 30, 40, 45, and 80. Eggs averaged 2.1 mm in diameter, were translucent, and contained a single oil droplet.

Ovaries of postspawning females collected in June and July were small compared to those of prespawning females collected from March through May (Fig. 5). Ovaries increased markedly in size between the

TABLE 2. - Relationship between size, age, and ovary weight of *Etheostoma kennicotti* females and the number of mature ova produced. An age of 1 year = 11-13 months, 2 years = 23-25 months.

Standard Length in mm	Adjusted Body Weight in Grams ^a	Age in Years	Ovary Weight in Grams	Number of Mature (Orange or Translucent) Ova
30	0.35	1	0.06	24
33	0.59	1	0.09	35
34	0.59	1	0.15	38
34	0.63	1	0.11	44
34	0.66	1	0.18	58
35	0.57	1	0.09	36
35	0.62	1	0.11	40
36	0.72	1	0.12	38
38	0.80	1	0.08	28
39	0.89	1	0.15	49
39	0.82	2	0.08	65
40	1.06	2	0.20	56
41	1.08	2	0.11	53
41	1.06	2	0.12	70
44	1.40	2	0.15	126
45	1.31	2	0.12	58
48	1.73	2	0.17	130

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

postspawning period and the spawning period the following spring. For the females examined, the relationship between the weight of the ovaries/the adjusted body weight (Y) and the month (X), with June = 1 and May = 12, was $\log Y = 0.500 + 0.130X$, with $r = 0.931$ (Fig. 5).

The proportionally largest ovaries (equalling 27.3 percent of the adjusted body weight) found were in a 1-year-old, 34-mm female collected on 16 April 1973. In the 17 females represented in Table 2, ovary-weight to adjusted-body-weight ratios ranged from 0.092 to 0.273 and averaged 0.152.

Spawning

E. kennicotti spawned on the undersides of the slab rocks (Fig. 6) previously selected and guarded as nesting territories by the males. In Big Creek, territories held by breeding males were found as early as 20 March, and nests with eggs were found from 5 April to 27 May. Most spawning occurred in late April or early May when water temperatures were from 14 to 20°C. Field observations and examinations of preserved specimens collected during all months of the year indicated April and May to be the spawning period throughout the range of the species (Table 3).

Nine spawnings of *E. kennicotti* captured in Big Creek occurred in laboratory aquaria; four were observed. Four of the nine spawnings occurred in the morning, four in the afternoon, and one during the night or early morning. Water temperatures varied from 19 to 22°C.

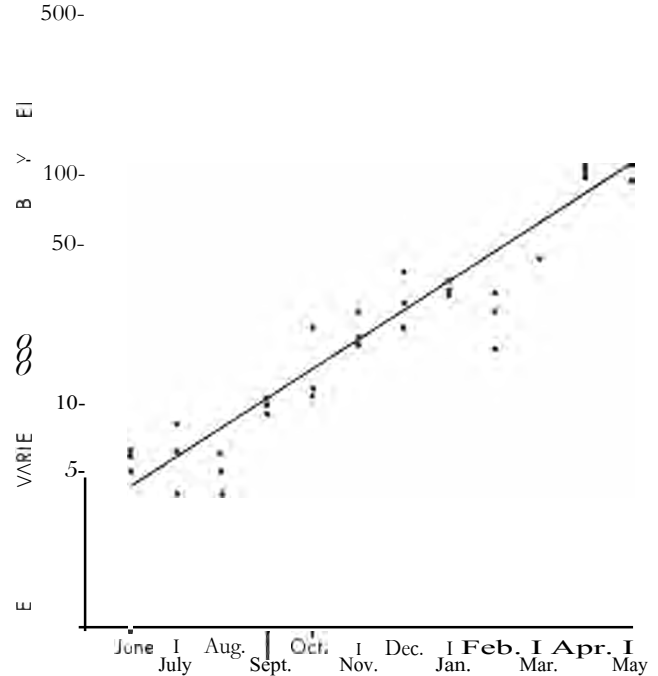


Fig. 5. - Monthly variations in ovarian weight relative to adjusted body weight of *Etheostoma kennicotti*. The vertical axis is on a logarithmic scale. Ovaries from specimens collected June to March were from 1+-year-old females (14-23 months), in April from 2-year-olds (24 months), and in May from 2+-year-olds (25 months).



Fig. 6. - Eggs of *Etheostoma kennicotti* on the underside of a stone removed from a slab pool in the headwaters of Big Creek on 22 April 1971.

Males left the nest stone to court females only briefly and only when a female was near the stone. In contrast, when a female swam under the stone she was vigorously courted by the male. Courting consisted mainly of the male laterally displaying his

TABLE 3.—Collections of breeding *Etheostoma kennicotti*.

Locality	Collection Date	Remarks
Big Creek, Hardin Co., Ill. (INHS)	17 April-3 May 1971	Spawning when collected.
Big Creek, Hardin Co., Ill. (INHS)	16 April-30 May 1973	Spawning when collected.
Big Creek, Hardin Co., Ill. (INHS)	5 April-21 April 1974	Spawning when collected.
Hunting Branch, Pope Co., Ill. (INHS)	19 May 1973	Spawning when collected.
Lick Creek, Union Co., Ill. (INHS)	19 May 1973	Females in extreme breeding condition.
Braden Branch, Anderson Co., Tenn. (UMMZ ^b 103697)	10 April 1937	Females in extreme breeding condition.
Creek, Anderson Co., Tenn. (UMMZ 103742)	26 April 1937	Females in extreme breeding condition.
Trib., Big South Fork, Scott Co., Tenn. (UT ^c 91,212)	26 May 1968	Females in extreme breeding condition.
Cusick Creek, Sevier Co., Tenn. (NLU ^d 19192)	22 April 1971	Females in extreme breeding condition.

^a Illinois Natural History Survey.

^b University of Michigan Museum of Zoology.

^c University of Tennessee.

^d Northeast Louisiana University.

breeding coloration and spread fins and wagging his tail near or against the female. Occasionally the male nudged the female with his snout.

When ready to spawn the female inverted underneath the nest stone by rolling to one side (Fig. 7). Females were observed to remain inverted for as long as an hour, during which time they rested by lowering their weight onto the substrate beneath the stone. When not resting, the female rose to the lower surface of the stone and darted over it in short, jerky movements, apparently selecting a site for egg deposition.

When laying eggs, the female pressed her genital papilla against the stone and was joined by the male who, after inverting by rolling to one side, positioned himself alongside and against the female, usually in a head-to-tail position and less often in a head-to-head position (Fig. 7). Both trembled as eggs and sperm were released. Then the male returned to an upright position and the female remained inverted. Some females were observed to lay eggs even though the male remained upright for an extended period.

During the trembling action of egg laying, which lasted 3–5 seconds, the female moved forward slightly, depositing one or two eggs. The periods between egg-laying sessions varied greatly and were perhaps prolonged due to the wariness of the fish while being observed. The eggs were laid in a concentrated area but never on top of one another.

As many as four females contributed to the aquarium nest of a male, but only one female at a time was allowed under the nest. Eggs by a second female were added to the egg mass began by the first female to spawn, and, as in *E. squamiceps*, the presence of eggs is probably a strong stimulus for females to spawn (Page 1974:14). In aquaria all females after the first to spawn added eggs only to the existing nest; no new nests were begun even though other males had established territories under stones and actively courted the females. One *E. kennicotti*

male spawned a second time after the eggs in his first nest had all hatched several days earlier.

Heavy feeding stimulated spawning in aquaria. Darters did not spawn when lightly fed but spawned readily after a heavy feeding of chironomid larvae.

Counts and estimates of the numbers of eggs in 12 nests of *E. kennicotti* found in Big Creek were 50, 80, 80, 85, 130, 200, 220, 300, 325, 325, 350, and 400 (mean = 212). Several of these nests contained more eggs than the largest number of mature ova (130) found in a preserved female and must have contained eggs from more than one female. Eggs in nests averaged 2.1 mm in diameter.

Males vigorously guarded the nest against invaders, including fishes and crayfishes slightly larger than themselves. When lifting a nest stone caused the male to leave the nest, he soon returned and again guarded the nest. Females did not guard the nests.

The breeding coloration of the male was retained during the very active period of nest guarding. The eggs were constantly examined visually by the male, who periodically nipped at the eggs, presumably to remove invading organisms or dead or diseased eggs. The continuous darting back and forth beneath the nest resulted in the eggs being constantly brushed by the dorsal fins.

The same slab pools used in Big Creek by *E. kennicotti* were used as spawning grounds by *E. squamiceps*, although spawning activity in *E. kennicotti* peaked slightly later (late April and early May for *E. kennicotti*; early April for *E. squamiceps*). *E. squamiceps* also utilized spring runs in Big Creek as spawning grounds whereas *E. kennicotti* did not. *E. kennicotti* utilized the rocky margins of deeper pools but *E. squamiceps* did not.

The spawning behavior of *E. flabellare* was described by Lake (1936) and by Winn (1958a, 1958b) and that of *E. squamiceps* by Page (1974). The behavior of *E. kennicotti* is more similar to that of *E. flabellare*. In both *E. kennicotti* and *E. flabel-*

Fig. 7. — *Etheostoma kennicotti* spawning in aquaria. In the top photo a female has inverted beneath a stone guarded by a male. In the bottom photo the male is inverting to position himself alongside the female.



lare, but not in *E. squamiceps*, the male and female normally align head-to-tail during egg laying, the females remain inverted between egg-laying sessions, and the male is usually intolerant of a right-side-up female under the nest stone.

Sexual Dimorphism

Twenty meristic and morphometric characters were tested for sexual dimorphism in 41 specimens over 45 mm from southern Illinois and adjacent Kentucky. In this sample, four characters showed significant ($P < .005$) sexual dimorphism. Females have a significantly higher number of pored lateral-line scales, and males have significantly deeper caudal peduncles, longer caudal fins, and longer soft dorsal fins. Sexual dimorphism in *E. kennicotti* in territorial behavior,

coloration, and size are discussed elsewhere in this paper.

DEVELOPMENT AND GROWTH

Eggs incubated in an aquarium at 19–23°C hatched in 145–150 hours (6.0–6.3 days). This incubation period is much shorter than that of *E. squamiceps* (11 days—Page 1974:11) and *E. flabellare* (20–30 days—Lake 1936:826) at a comparable temperature range. Eggs from only one nest were kept alive to hatching.

Hatchlings of *E. kennicotti* (Fig. 8) were 5.7 mm in total length and mostly translucent with only a few melanophores. They had the same well-developed lower jaw and pectoral fins characteristic of *E. squamiceps* (Page 1974:11) and *E. flabellare* hatchlings

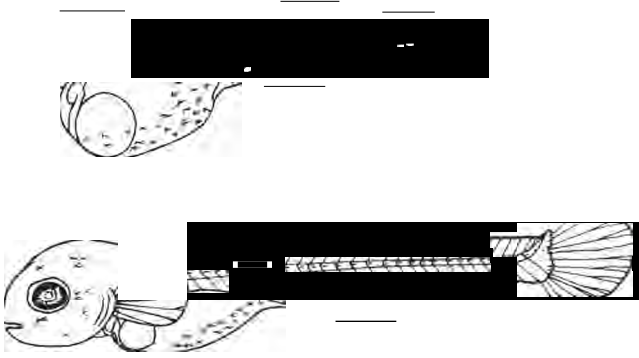


Fig. 8. - *Etheostoma kennicotti* hatchling (5.7 mm total length) and 3-day-old larva (7.2 mm total length).

(Lake 1936:826-827). The spines and rays of the median fins were evident by the third day (Fig. 8).

A series of 39 young *E. kennicotti* ranging from 10 to 20 mm was collected in the study area on 20 July 1971. The color pattern of individuals up to 15 mm consisted of relatively large, dark spots on the sides and dorsum. On specimens over 15 mm the pattern approached that of an adult (Cover Illustration) but the lateral spots remained and the mottling on the dorsum was more subdued than in adults.

Squamation was nearly complete at 10 mm, the scales normally found on the adult being absent only on the belly and anterior dorsum to below the first dorsal fin. At 15 mm, squamation was complete. The lateral-line canal began forming at about 15 mm and at 18 mm extended to beneath the first dorsal fin.

Big Creek *E. kennicotti* grew at a decreasing rate (Fig. 9). The relationship between standard length (Y) and age in months (X) is expressed for males by the equation $Y = -3.11 + 33.02 \log X$, with $r = 0.939$, and for females by the equation $Y = -3.37 + 31.55 \log X$, with $r = 0.911$.

Males grew more rapidly than females (Fig. 9) and by the third year were significantly larger than

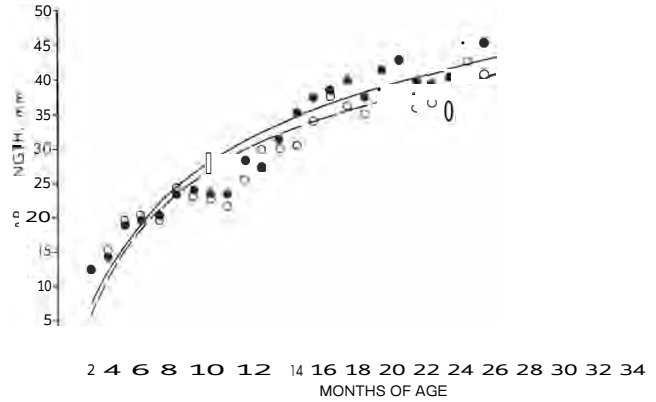


Fig. 9. - Size distribution by age of *Etheostoma kennicotti* collected in Big Creek between 6 October 1970 and 19 June 1973. Black dots represent sample means for males; circles represent sample means for females. In total, 1,380 specimens are represented.

females ($t = 3.46$, $df = 44$). The largest specimen examined from Big Creek was a 54-mm male collected on 25 March 1972. In the upper Cumberland River system *E. kennicotti* gets considerably larger, and specimens as long as 69 mm have been collected. Table 4 presents the standard lengths of 1- and 2-year-old *E. kennicotti* collected in April 1971 and 1973.

E. kennicotti reached one-half of the first year's mean growth in approximately 16 weeks; this is a longer period than required for *E. squamiceps* (12 weeks — Page 1974:12) and much longer than that required for *E. gracile* (1 week — Braasch & Smith 1967:9) and *Percina phoxocephala* (2 weeks — Page & Smith 1971:9).

DEMOGRAPHY

Density

On four separate dates at approximately 3-month intervals, quantitative samples of *E. kennicotti* were taken in Big Creek by repeatedly seining measured areas of stream until no more individuals were col-

TABLE 4.-Standard lengths of *Etheostoma kennicotti* collected in Big Creek at 1 and 2 years (12 and 24 months) of age. Specimens were collected in April 1971 and 1973.

Sex and Collection Year	Age	Number	Standard Length		
			Mean	Range	Standard Deviation
Males 1971	1	25	25.9	18.9-35.9	4.7
Males 1973	1	5	34.8	31.0-38.1	2.8
Females 1971	1	54	29.7	19.4-43.5	6.1
Females 1973	1	11	32.9	28.2-39.8	3.7
Males 1971	2	13	45.0	39.8-49.7	3.1
Males 1973	2	3	48.7	47.2-51.4	2.3
Females 1971	2	8	41.8	40.3-43.4	1.4
Females 1973	2	6	43.5	38.3-47.5	3.5

lected. The number collected was transposed into the number per square meter (Table 5).

The highest densities of both young and adults were consistently found in the slab pools, previously noted to be the preferred habitat of *E. kennicotti* (Table 1). With young and adults combined, the greatest density found for *E. kennicotti* in Big Creek was in the slab pools in July (6.5 per m²).

TABLE 5. - Number of *Etheostoma kennicotti* per square meter collected in Big Creek at approximate 3-month intervals, by habitat. Young were up to 1 year of age, adults over 1 year.

Date	Number Collected	Number of <i>E. kennicotti</i> per Square Meter in		
		Slab Pools	Gravel Riffles	Non-slab Pools
Adults				
8 July 1972	36	4.71	0.09	0
19 October 1972	35	1.71	0.63	0.97
17 January 1973	11	1.21	0	0
16 April 1973	9	0.95	0.22	0.12
	Mean	2.15	0.24	0.27
	SD	1.74	0.28	0.47
Young				
8 July 1972	17	1.75	0	0.23
19 October 1972	17	1.23	0.63	0.26
17 January 1973	10	1.10	0	0
16 April 1973	16	1.61	0	0.47
	Mean	1.42	0.16	0.24
	SD	0.31	0.32	0.19

Composition

Of the 1,380 *E. kennicotti* collected in Big Creek, 55.7 percent were up to 1 year of age, 41.0 percent were over 1 and up to 2 years of age, and 3.3 percent were over 2 years (Table 6).

Females predominated in the young-of-the-year (-1) age class [1.4 females to 1 male ($\chi^2 = 18.13$; $P < 0.005$)], in the 1+ year class [1.7 to 1 ($\chi^2 = 36.64$; $P < 0.005$)], and in the total sample [1.5 to 1 ($\chi^2 = 47.49$; $P < 0.005$)]. Although predominating significantly in the younger age classes, females were slightly less common than males in the 2+ year class, reflecting the same greater longevity of males found in other darters (e.g. *E. squamiceps* - Page 1974:13).

TABLE 6. - Distribution of sexes and year classes in samples of *Etheostoma kennicotti* collected between 6 October 1970 and 19 June 1973.

Sex	Number by Year Class			Total
	-1	1+	2+	
Males	325	211	26	562
Females	443	355	20	818
Total	768	566	46	1,380

For *E. squamiceps* a relationship was suggested (Page 1974:13) between the predominance of females and the reduced need for a 1:1 sex ratio during spawning (because only the large males of *E. squamiceps* spawn and because several females may contribute to the nest of one male). Although small as well as large *E. kennicotti* males spawn, probably most successful spawnings are accomplished by the larger males because of the importance of holding a breeding territory, and a reduced necessity for a 1:1 sex ratio during spawning may also be characteristic of *E. kennicotti*.

Survival

Relative survival values (Table 7) for each year of life were calculated for males, females, and total samples of *E. kennicotti*, using the data in Table 6. It was assumed that each age class was collected in proportion to its relative number in the population, that the population was neither increasing nor decreasing, and that the number of fry entering the population each year was constant.

Because approximately one-third of the sampling effort each month was expended in the slab pools, which constitute less than one-third of Big Creek but in which adults tended to be concentrated (Tables 1 and 5), the number of adults in Table 6 probably exaggerates their actual proportion in the population. Survival was therefore computed on the 1+ year class as well as the -1 year class (Table 7).

The shapes of the survival curves for males, females, and total samples (Fig. 10) were similar. All showed a very low survival rate for *E. kennicotti* during the third year of life. No individuals 3 years or older were found and the maximum life-span of *E. kennicotti* in Big Creek is apparently 2+ years. In contrast, the related *E. squamiceps* had a maximum life-span of 3+ years in Big Creek (Page 1974:13-14). The oldest *E. kennicotti* from Big Creek examined were four males 2 years and 9 months old (assuming April hatchings) collected in January of 1971 and 1973.

TABLE 7. - Relative survival of year classes of *Etheostoma kennicotti* expressed as proportions of the -1 year class ($1x^1$) and the 1+ year class ($1x^2$).

Sample	Year Class	Number of Specimens	Survival	
			$1x^1$	$1x^2$
Males	-1	325	1.000	
	1+	211	0.649	1.000
	2+	26	0.080	0.123
Females	-1	443	1.000	
	1+	355	0.801	1.000
	2+	20	0.045	0.056
Total sample	-1	768	1.000	
	1+	566	0.737	1.000
	2+	46	0.060	0.081

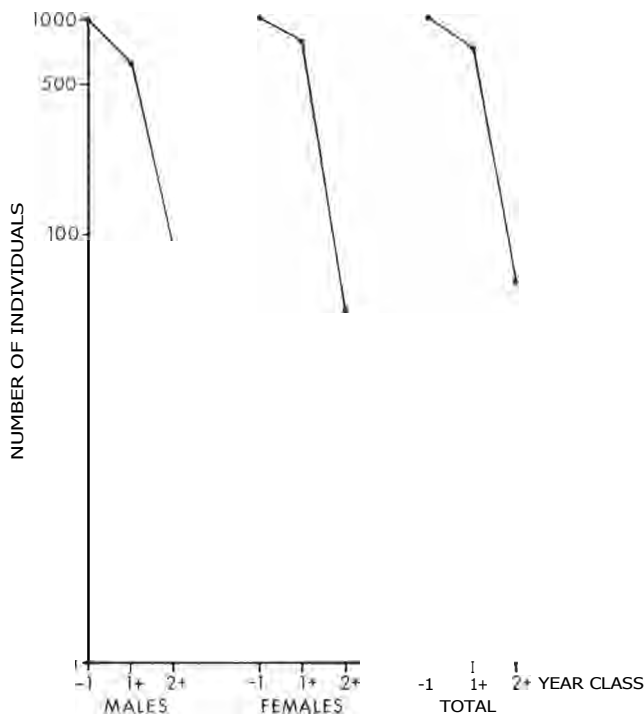


Fig. 10. — Survival curves for *Etheostoma kennicotti* based on the data in the 1 \bar{x} column in Table 7 multiplied by 1000. The vertical axis is a logarithmic scale.

Migration

Most spawning occurred in upstream headwater pools; this probably necessitated movement upstream by some individuals prior to the spring spawning period, and possibly a subsequent downstream dispersal during summer or fall. However, both young and adults were most common in slab pools during all seasons (Table 1) and no obvious migrating patterns were noted for *E. kennicotti*.

Territoriality

Observations made on aquarium-held *E. kennicotti* and in the study area indicated that males are strongly territorial, especially during the spawning season, and that females are occasionally territorial. When defending a territory, the male has a darkened head and prominent vertical bars, and the first dorsal fin is held erect, displaying the brilliantly colored gold knobs.

Territories were most vigorously defended during the spawning season and centered about the nest stone. Combats were common and consisted of threat displays (a lateral display in a slight angle with the head lower than the caudal fin, the median fins erect, and the lateral vertical bars prominent), nipping, and tail slapping. Often two combating males circled rapidly, each nipping the tail of the other. The selective advantage for territoriality during the spawning season is evident; as in *E. squamiceps*, the first male to spawn in an aquarium was the only male to spawn.

As in *E. squamiceps* (Page 1974:14) aquarium-held *E. kennicotti* females in the area away from the nest stones became belligerent toward other females and defended nonstationary territories. The coloration of a territorial female is similar to that on a territorial male, with vertical bars and a darkened head, but less well developed.

DIET

Stomach contents of 333 *E. kennicotti* were examined. The contents consisted mostly of immature insects and small crustaceans (Tables 8 and 9), with the predominant food items being chironomid larvae, copepods, mayfly naiads, cladocerans, and ostracods. The variety of food items was less (16 versus 22 taxa) than that found for *E. squamiceps* in the same study area (Page 1974:14-18) even though more specimens of *E. kennicotti* (333 versus 173) were examined. *E. squamiceps* attains a larger size (72 mm standard length) than *E. kennicotti* (54 mm) in Big Creek and therefore can presumably ingest a greater variety of food items.

Small *E. kennicotti* (<21 mm) fed mainly on mayflies, copepods, chironomids, and ostracods; the large ones (>40 mm) fed mainly on mayflies, chironomids, isopods, and amphipods (Table 8).

Some seasonal variation in diet (Table 9) was evident among the 142 specimens of *E. kennicotti* ranging from 31-40 mm (the size class having the largest number of individuals). Chironomids were the major food component during winter and spring; mayflies were the major component from July to November. Stoneflies were heavily consumed in December and January but were absent in the diet from March to November. Food consumption was heaviest in December, January, and March.

E. kennicotti fed in the same way as described for *E. squamiceps* (Page 1974:17), and aquarium-held darters, including nest-guarding males, fed readily on frozen earthworms and live aquatic insects and crustaceans.

INTERACTIONS WITH OTHER ORGANISMS

Competition

In contrast to *E. squamiceps*, which occurs syntopically with all other described species of *Catonotus*, *E. kennicotti* appears to be limited in distribution, abundance, and size at least in part by the distributions of other species of the subgenus *Catonotus*. This will be examined in more detail by Page and P. W. Smith in a paper on geographic variation in *E. kennicotti*.

The use by *Catonotus* species of slab-rock pools as spawning grounds, and their dependence on slab rocks during all stages of their life histories (Lake 1936, Winn 1958a, 1958b, Page 1974) seem to result in

TABLE 8.—Stomach contents of *Etheostoma kennicotti* from Big 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 (22)	21-30 mm (90)	31-40 mm (142)	41-50 mm (77)	>50 mm (2)	<21 mm (22)	21-30 mm (90)	31-40 mm (142)	41-50 mm (77)	> ⁵⁰ mm (2)
Oligochaeta				1.3					0.01	
Gastropoda			0.7	1.3				0.01	0.01	
Crustacea										
Cladocera	9.1	10.0	2.1	1.3		0.23	1.79	0.11	0.01	
Ostracoda	13.6	8.9	3.5	5.2		1.14	0.19	0.08	0.12	
Copepoda	68.2	33.3	9.9	9.1		2.27	2.11	0.19	0.13	
Isopoda										
Asellidae		8.9	6.3	18.2			0.10	0.06	0.26	
Amphipoda	4.5	5.6	12.0	14.3		0.05	0.07	0.13	0.19	
Insecta										
Plecoptera		14.4	9.2	5.2			0.32	0.39	0.16	
Ephemeroptera	86.4	44.4	46.5	53.2		1.45	0.72	0.64	0.78	
Odonata										
Anisoptera		1.1	0.7				0.01	0.01		
Megaloptera					50.0					0.50
Trichoptera	4.5		7.0	5.2	50.0	0.05		0.08	0.08	0.50
Coleoptera										
Psephenidae			0.7					0.01		
Others	4.5	6.7	1.4	5.2		0.05	0.07	0.01	0.06	
Diptera										
Chironomidae	50.0	62.2	51.4	42.9	100.0	1.00	2.91	2.85	2.70	3.00
Others			3.5	5.2				0.04	0.05	

competition among the species. Although differences in nonspawning habitat preference may be recognized, all species studied utilize slab pools as spawning grounds and, when syntopic, probably compete for space. The staggering of spawning periods (Page 1974:18) may help reduce competition among certain species.

Predation

No information on predation on *E. kennicotti* has been published, and there was no evidence of predation in this study. As potential predators five *Esox americanus* and 12 *Lepomis cyanellus* collected with *E. kennicotti* in Big Creek were preserved and later examined. No ingested *E. kennicotti* were found.

Parasitism

Three piscicolid leeches were found on the caudal and pectoral fins of eight of the *E. kennicotti* collected from Big Creek during October (1970 and 1971) and November (1970). No other ectoparasites were noted on the 1,380 specimens examined.

In the 333 specimens from which stomach contents were examined, 33 contained a total of 63 spiny-headed worms (presumably *Acanthocephalus jacksoni*) in their intestines. This is a much lower infestation than was found in *E. squamiceps* in the same

study area (Page 1974:19). As in *E. squamiceps*, more worms were found in the larger *E. kennicotti* (up to 5 worms). In *E. kennicotti*, infestation occurred only from November through March. The absence of worms in specimens collected from June through October is similar to the infestation pattern found in *E. squamiceps*.

Hybridization

The only known hybrid of *E. kennicotti* is a 40-mm *E. squamiceps* x *E. kennicotti* male, described by Page (1974:19-20) and shown in Fig. 11.

Species recognition during spawning apparently depends mainly on visual cues perceived by the female, as the color and courting behavior of the breeding male suggest. In aquaria, male *E. kennicotti* were observed courting females of *E. squamiceps* and *E. obeyense*, and on two separate dates spawning occurred between a male *E. kennicotti* and a female *E. obeyense*. The eggs hatched but the young lived only a few days.

SUMMARY

The life-history information on *E. kennicotti* collected in Big Creek between 6 October 1970 and 21 April 1974 is summarized in Table 10.

TABLE 9.-Stomach contents of *Etheostoma kennicotti* ranging in size from 31 to 40 mm from Big 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. (10)	Feb. (17)	Mar. (15)	Apr. (13)	May (22)	June (1)	July (10)	Aug. (19)	Sept. (7)	Oct. (10)	Nov. (8)	Dec. (10)	Jan. (10)	Feb. (17)	Mar. (15)	Apr. (13)	May (22)	June (1)	July (10)	Aug. (19)	Sept. (7)	Oct. (10)	Nov. (8)	Dec. (10)
Gastropoda							..	14.3											..	0.14				
Crustacea																								
Cladocera		..	13.3							..	12.5		..	1.00					0.13			
Ostracoda				..	13.6	..	10.0	..	14.3						..	0.23	..	0.40	..	0.43				
Copepoda	40.0	11.8	..	30.8	13.6						..	10.0	0.90	0.18	..	0.77	0.18						..	0.10
Isopoda																								
Asellidae	..	11.8	6.7	..	4.5		..	10.5	..	20.0	12.5	20.0	..	0.12	0.07	..	0.05		..	0.11	..	0.20	0.13	0.20
Amphipoda	10.0	5.9	6.7	30.8	18.2	..	10.0	10.5	..	30.0	..		0.10	0.06	0.07	0.38	0.23		0.10	0.11	..	0.30	..	
Insecta																								
Plecoptera	40.0	11.8	70.0	1.70	0.12	3.60	
Ephemeroptera	20.0	76.5	26.7	61.5	50.0	..	50.0	36.8	57.1	70.0	87.5	40.0	0.50	1.00	0.40	0.85	0.50	..	0.30	0.47	0.86	1.30	1.25	0.60
Odonata																								
Anisoptera	10.0	0.10			
Trichoptera	10.0	17.6	20.0	7.7	4.5					..	25.0		0.10	0.18	0.20	0.15	0.05					..	0.25	
Coleoptera	10.0	4.5				..	10.0	..		0.10	0.05			..	0.10			
Diptera																								
Chironomidae	70.0	64.7	100.0	92.3	45.5	..	20.0	15.8	14.3	10.0	12.5	100.0	7.20	2.12	12.00	2.23	1.41	..	0.20	0.21	0.43	0.10	0.50	5.70
Others	6.7	15.4	9.1		..	10.5	0.07	0.15	0.09		..	0.11	..			

Fig. 11. — Hybrid *Etheostoma squamiceps* x *E. kennicotti*.



TABLE 10.—Summary of life-history information on Big Creek *Etheostoma kennicotti*.

Characteristic	Life-History Data
Principal habitat of adults	Slab pools
Principal habitat of young	Slab pools
Age at reaching sexual maturity	1 year
Age at first spawning	1 year
Size at reaching sexual maturity	Females about 30 mm; males about 35 mm
Sexual dimorphism	Adult males average larger, are more boldly patterned in spring, and have longer fins and a deeper caudal peduncle; females have a larger number of pored lateral-line scales
Breeding tubercles	Absent
Number of mature ova in preserved females	24-130
Description of egg in nest	2.1 mm in diameter, translucent, adhesive
Spawning period	From early April to late May
Spawning habitat	Slab pools
Spawning position	Both male and female inverted, usually head-to-tail
Nesting site	Underside of a slab stone
Number of eggs counted in nests	50-400
Egg guarding	Only by the male
Incubation period	145-150 hours at 19-23° C
Influence of sex on growth rate	By the third year males are significantly larger than females
Density	Up to 6.5 darters/m ² in slab pools
Sex ratio among young	1.4 females : 1 male
Longevity	2+ years
Maximum size	54 mm standard length
Migrations	No obvious patterns
Territoriality	Extreme in breeding males; strong in nonbreeding males; occasional in females
Principal diet	Aquatic insect immatures and crustaceans

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