Southeastern Fishes Council Proceedings

Volume 1
Number 23 *Number 23 (February 1991)*

Article 2

2-1-1991

Life History of the Brighteye Darter *Etheostoma Lynceum* (Pisces: Percidae), in Terrapin Creek, Kentucky

Dianna Bell

Tom J. Timmons

Life History of the Brighteye Darter *Etheostoma Lynceum* (Pisces: Percidae), in Terrapin Creek, Kentucky

Southeastern Fishes Council
PROCEEDINGS
DEDICATED TO THE PRESERVATION OF SOUTHEASTERN FISHES

Number 23 February 1991

LIFE HISTORY OF THE BRIGHTEYE DARTER *ETHEOSTOMA LYNCEUM* (PISCES: PERCIDAE), IN TERRAPIN CREEK, KENTUCKY

Diana Bell and Tom J. Timmons

Department of Biological Sciences
Hancock Biological Station
Murray State University
Murray, Kentucky 42071

ABSTRACT

The brighteye darter, *Etheostoma lynceum* (Hay), is limited to eastern tributaries of the lower Mississippi River below the Fall Line. *E. lynceum* from Terrapin Creek, Graves County, Kentucky, was studied from January 1983 through December 1983. It was collected in undercut stream banks with dense tree roots in winter and in fast flowing, shallow, gravel riffles in summer. Chrinomids were the predominant food item (50% by volume; 68-100% frequency of occurrence). Feeding was diurnal, peaking at 1700 hrs. Adult and juvenile brighteye darters ate the same bottom invertebrates, but juveniles ate smaller and fewer items. The reproductive season extended from April into June. The bright green coloration of the vertical bands, fins, breast, and belly was more intense in males than females. Females exhibited greatly enlarged genital papillae during breeding and could be sexed externally. Fecundity varied from a range of 33-116 mature ova for age I fish to 65-201 for age III. Ripe ova were 1.1 to 1.6 mm in diameter, translucent, yellow, and appeared as early as February. Both sexes attained age III, and the oldest fish was a female (44 mm) approximately 3.5 years old.

INTRODUCTION

The brighteye darter, *Etheostoma lynceum* (Hay), was formerly one of two recognized subspecies of *E. zonale* (Tsai and Raney 1974). The difference in appearance and meristic characters between *E. zonale* and the allopatric *E. lynceum* have been discussed in depth by Etnier and Starnes (1986). The distribution of *E. lynceum* is limited to eastern tributaries of the lower Mississippi River below the Fall Line in Kentucky and Tennessee (Obion, Hatchie and Wolf river systems) and Mississippi (Yazoo,Black and Homochitto river systmes); and in eastern Gulf slope drainages in Mississippi and Louisiana (Tangipahoa, Pearl and Pascagoula river drainages). *E. zonale* is found in the Mississippi River drainages above the Fall Line, western drainages of Lake Michigan, and headwaters of the Savannah River on the Atlantic slope (Tsai and Raney 1974).

The life history of *E. zonale* has been described from several regions: Pennsylvania (Lachner et al. 1950), Ohio (Adamson and Wissing 1977), Minnesota (Erickson 1977), West Virginia (Holbrook and Tarter 1977), New York (Nemecek 1980), and Illinois (Cordes and Page 1980). There have, however, been no studies on the life history of *E. lynceum*. The objective of this study was to provide information on the life history of this new species, not only for comparison to *E. zonale*, but also because the habitat of the brighteye darter is often destroyed by channelization and the adverse impacts from intensive agricultural practices. *Etheostoma lynceum* is found in Kentucky only in Terrapin Creek, a stream included in the list of Outstanding Resource Waters by the Kentucky Nature Preserves Commission (Hannan et al. 1982).

MATERIALS AND METHODS

Specimens of *E. lynceum* were collected from Terrapin Creek, Graves County, Kentucky with a 3-m long seine from January to December 1983 and preserved in 10% formalin. Data recorded on field conditions included depth and width of stream sites, description of substrate type and size, presence of vegetation or cover, and water temperature. Flow was measured using a Teledyne Gurley water current meter.

Each fish was blotted dry with a paper towel and weighed to the nearest 0.001 g on a Mettler analytical balance. The standard length (SL) was measured to the nearest 0.1 mm with a dial caliper and the sex was determined. Scales were removed from the right side above the lateral line and near the junction of the soft and spinous dorsal fins. The scales were mounted between glass slides and viewed with a microprojector. Fish were assigned to age groups by counting the annuli. Age class designations consisted of 0-III years, with fish spawned in the spring or summer considered to be age class 0 until January 1.

The population density (number of fish/m²) of *E. lynceum* was estimated on 6 September 1983 by the Leslie method (Leslie and Davis 1939). A 12-m long section of stream, with a surface area of 24 m² and an average depth of approximately 0.3 m, was sampled. The length of the stream section between two 5-mm mesh block nets was sampled by numerous short seine hauls on each sample until only a few fish were collected per 24 m² sample. Fish were identified, counted, and released below the downstream block net. The number of seine hauls per sample was constant. A regression line was then projected to the intercept of the X-axis to estimate the population size.

Changes in the ova diameters and ovarian weights were observed. Ovaries were removed and weighed to the nearest 0.001 g. Ovarian weight was calculated as a percentage of the somatic body weight. Ova, taken from fish collected from April through July, were separated from other ovarian tissue and measured with a calibrated ocular micrometer. Fecundity was determined by direct counts of mature ova.

Feeding habits of *E. lynceum* from Terrapin Creek were evaluated by removing contents of the digestive tract anterior to the intestine and examining them under a dissecting microscope. Food items from each fish were identified, counted, and their relative volumes estimated using an ocular micrometer. Volume was estimated because numerical analysis may overemphasize the importance of small food items (Windell 1971). The frequency of occurrence of food items and the percent volume of a food item were calculated.

The feeding periodicity of *E. lynceum* was determined by seine collections at 3-hr. intervals from 0500 hrs on 13 July to 0200 hrs on 14 July. Drift and bottom invertebrates were sampled every three hours using Surber samplers and drift nets set upstream from the area seined for darters. Drift nets were left in the latter and checked every three hours.

Study Site

Terrapin Creek is a tributary of the North Fork of the Obion River in Graves County in western Kentucky. The study site was 4.2 km upstream from its mouth and 3.2 km south of Bell City. County road number 1270 crosses the creek at the study site. The creek bottom was shifting sand and fine and medium-sized gravel without a constant pool to riffle ratio. It was common in some areas to sink 0.3 m into the loose sand and gravel while walking in the stream. The loose bottom allowed the stream to meander and constantly change within the banks. The study site consisted of pools less than 1 m in depth, riffles, and undercut banks. Except in winter, the tree-lined banks shaded the entire stream. Aquatic macrophytes were absent and fallen trees and tree roots were the only cover in the pools. Water overflowed the 3-m banks into nearby farmland and woods after heavy rainfall. Small springs flow into Terrapin Creek, and it was one of the few streams still flowing during the severe summer drought in 1983. The inflow of spring water keeps the temperature cool during the summer (maximum of 22.2° C) and ice free in the winter (minimum of 4.4° C). The discharge was 33 cfs and the velocity was 0.63 m/s on 6 July 1983. A list of fish species known from Terrapin Creek appears in Burr and Warren (1986).

RESULTS AND DISCUSSION

Life History

In the winter, *E. lynceum* specimens were collected in water 0.3-0.6 m deep with moderate current among dense tree roots beneath the undercut banks. Also common in seine hauls with the brighteye darter were *Lampetra aepyptera* ammocoetes, *Semotilus atromaculatus*, *Erimyzon oblongus*, *Aphredoderus sayanus*, *Etheostoma nigrum*, and *E. pyrrhogaster*. During the summer the brighteye darter moved into the shallow gravel riffles. They were commonly collected in riffles with *E. nigrum* and *E. pyrrhogaster*. Young-of-the-year brighteye darters were found over a solid gravel bottom in the lower portion of a riffle as it entered a pool. They were commonly collected with young-of-the-year *E. nigrum*, *E. pyrrhogaster*, and several cyprinids.

The density of brighteye darters was estimated to be 4.2 fish/m². The projected regression line (r = 0.88) indicated 100 brighteye darters per 24/m². The density of the second most abundant darter, *E. nigrum*, was estimated to be 44 per 24/m² (r = 0.98).

The monthly, mean standard length of each group by sex was determined for 406 *E. lynceum*. Little growth occurred from October through May for most brighteye darters. The most rapid growth occurred between June and August. After the second year males were longer than females of the same age. Age II fish were absent or poorly represented in samples throughout the year. Annuli were readily identified on scales by changes in spacing of circuli and cutting over of circuli at edges of lateral fields. It is unlikely that age II fish were not recognized. A poor spawning season or destruction of eggs or young from floods may account for reduced numbers of that year class. Matthews (1986) documented alterations of species compositions during a catastrophic flood in the Piney Creek watershed in Arkansas. He noted that benthic species in riffles showed the least reduction in numbers during the December flood. Young-of-the-year centrarchids and cyprinids were extremely susceptible to downstream displacement by flooding in Brier Creek, Oklahoma (Harvey 1987). John (1964) observed that flash floods in streams of the Chiricahua Mountains, Arizona, could annihilate, or at least displace downstream, a fish population, especially young of the year. Occasional spring floods in Terrapin Creek raise the water level more than 3 m and may have been responsible in 1981 for the missing age II darters. A flood at spawning time could wash away or destroy eggs, since the loose gravel bottom of Terrapin Creek must move and be churned to a considerable depth during floods.

Of the 406 fish for which the age was determined, 12.1% were age 0, 69.0 % were age I, 2.4% were age II, and 16.5% were age III. Males of age 0-III represented 14.5%, 68.3%, 4.1% and 13.1%, respectively. Females age 0-III represented 7.5%, 71.8%, 1.6%, and 19.0%. Age I fish of both sexes comprised the greatest percentages. Sixty-seven brighteye darters were in age group III. Assuming an April spawn, the oldest fish was a 44.3 mm female, 3.5 years of age, collected November 1983.

The sex ratios (male:female) were determined for all bright eye darters (1:1.7) and by age groups. At age 0 there was no significant departure from 1:1 ratio ($X^2 = 0.10$, $0.90<P<0.75$). Females did outnumber males at age I (1:1.8, $X^2 = 24.01$ $P<0.001$)

and age III (1:2.5, $X^2 = 12.55$, $P<0.001$). This could indicate either an accelerated male mortality rate or sampling bias of males because of preferential habitat selection. At age II, males outnumbered females (1:0.67, $X^2 = 0.40$, $0.70<P<0.50$). Values for the age group II may not be accurate because of the small sample size.

Breeding males attained greater lengths than females of the same age, and displayed more intense green coloration of the vertical bands, fins, breast, and belly than females. In both sexes, the green coloration persisted most of the year, and was least intense in the fall. The intensity of coloration increased not only within females and males, but also with age, the oldest fish being the deepest green. Mature females exhibited greatly enlarged genital papillae (upon intensification of breeding coloration) and could be sexed externally. The abdomens of females started to enlarge by February, and eggs were expelled with slight pressure on the abdomen in April. All females collected by August were spent.

The percent of the body weight contributed by the ovaries (Gonadosomatic Index or GSI) was compared monthly for the degree of ovary maturity. The GSI increases until the start of spawning, at which time there is a distinct decrease with the smallest percentages occurring when spawning activity ends (Pickford and Atz 1957). GSI decreased after the peak of 12% in April (Fig. 1), indicating the start of spawning when the water temperature was 18°C. The lowest value (1%) was in August, indicating the time spawning was completed. The slight increase from May to June may have resulted from an interruption of spawning by flooding as has been observed in *Etheostoma tetrazonum* in Missouri (Taber and Taber 1983).

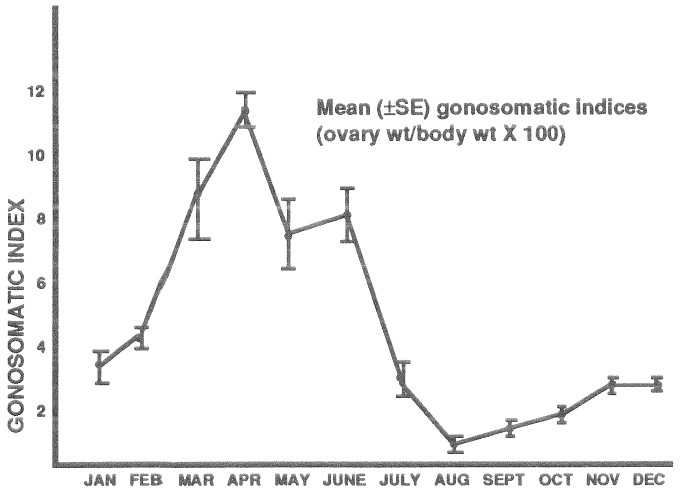


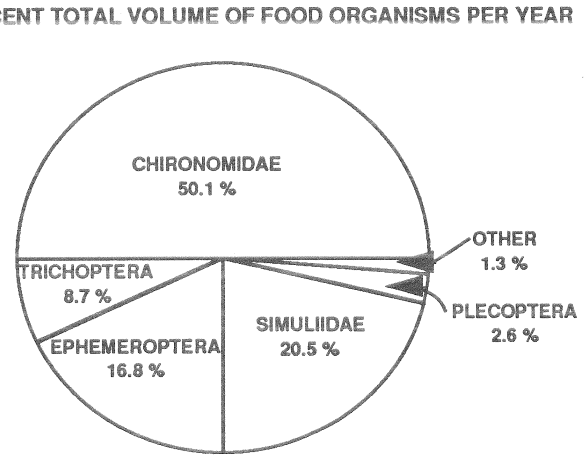
Figure 1. Mean monthly percent of body weight contributed by the ovary for brighteye darters in Terrapin Creek, January through December, 1983.

The ovarian development was followed throughout the year. Only small, white, immature ova less than 0.7 mm in diameter were present in August. These ova started to mature in October and continued to do so during the winter months. Maturing ova were yellow and 0.7-1.1 mm in diameter. Ripe ova (1.1-1.6 mm in diameter and translucent) were present as early as February. All three types of ova were present through the possible spawning months of April to July. The ova may have continued to mature during these months, being spawned as they became ripe. Spawning was complete for most fish by the end of June since most of the ovaries were spent in July. Young of the year were not collected until 27 August 1983. Those collect 6 September (n = 9) ranged in size from 12.9 to 22.8 mm (SL).

Spawning activity was not observed in the stream or in aquaria. Bright eye darters lived successfully in aquaria from May until November when they were released. Many darters have been observed to spawn successfully in aquaria (New 1966, Braasch and Smith 1967, May 1969, Seesock 1979, Ryon 1986).

Examination of ova size-frequency distribution indicated ova greater than 0.6 mm were spawned, and there was no sign of reabsorption. Fecundity was estimated for fish collected in April, May, and June. Females attaining age I and which were also at least 27 mm SL were capable of spawning. Females were either age I or age III, and fecundity ranged from 21-116 for age I to 65-201 for age III. Males were also sexually mature at age I.

The predominant foods of *E. lynceum* were Diptera (Chironomidae and Simuliidae), Ephemeroptera nymphs, and Trichoptera larvae (Fig. 2). The most abundant food item was chironomid larvae, (50% by volume and 67 % frequency of occurrence (Table 1). Chironomids did not make up the greatest volume every month (Table 2). The greatest volume was Simuliidae larvae in June (75.3%), Ephemeroptera in October (54.6%), and Trichoptera in November (53.4%). Of the stomachs examined, 19.8% were empty. Adults and juveniles consumed the same food items, but juveniles ate fewer and smaller organisms.



The brighteye darter in Terrapin Creek had a diurnal feeding pattern, with a peak in volume and number of food items at 0500 hrs and 1700 hrs (Fig 3). Feeding began at or just before sunrise (0500 hrs), decreased after three hours, and increased to peak at 1700 hrs. Feeding decreased in the early evening and stopped after sunset (2100 hrs). After sunset, all stomachs were empty or contained extremely digested insect larvae.

Dipteran and Ephemeroptera larvae were the most abundant food items in stomachs and in invertebrate samples made during the 24-hour study. Food items in the stomach of brighteye darters were those invertebrates predominantly found in the Surber samples. The greatest number of invertebrates was found at 2300 hrs in both

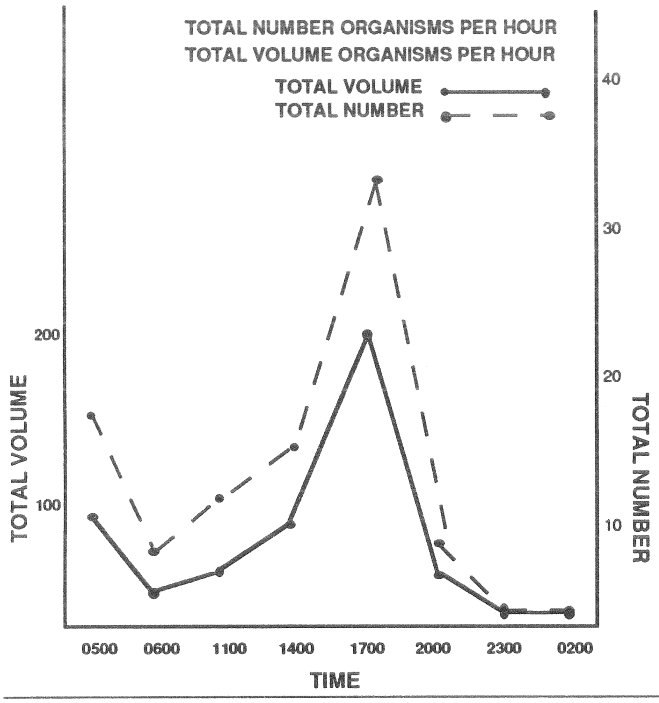


Figure 3. Total number and volume of food organisms per three hour period in brighteye darters from Terrapin Creek, during a 24-hr study on 6 September 1983.

Surber and drift net samples. The brighteye darter did not feed at night and could not take advantage of the great number of invertebrates present in the night samples.

Comparison of *E. zonale* and *E. lynceum*

Published life history information for *E. zonale* was compared with our data for *E. lynceum* in Terrapin Creek. *E. zonale* is typically found in riffle areas of larger streams (usually order 4 or larger), over large gravel or rubble and is often associated with aquatic vegetation (Lachner et al. 1950, Erickson 1977, Nemecek 1980). Whereas, we found *E. lynceum* in smaller streams (order 2 or 3) with fine to medium gravel and sand bottoms and utilizing existing cover of undercuts. Brighteye darter young-of-the-year were first observed at the edge of pools below riffles, whereas Erickson (1977) observed young-of-the-year banded darters in sand-gravel substrate in slow moving water 30-50cm in depth below a large riffle.

E. zonale has its highest growth rate in the first year (Lachner et al. 1950, Lutterbie 1976) and fastest growth during the summer (Erickson 1977). *E. zonale* survives to age IV in both Wisconsin (Lutterbie 1976) and Minnesota (Erickson 1977) and reach a maximum of size of 62 mm SL in Pennsylvania (Lachner et al. 1950). *E. lynceum* also achieves greatest growth in the first year during June to August. The oldest fish was estimated to be 3.5 years, and the largest specimen was 52 mm SL.

Nemecek (1980) observed *E. zonale* laying eggs on algae (Cladophora) in water depths of 15-30 cm, and water temperatures of 18.5 to 22.0° C. Some age I fish are capable of spawning (Lachner et al. 1950,Erickson 1977). Spawning of the banded darter has been reported from late March to June (Lachner et al. 1950, Cross 1967, Miller and Robinson 1973, Lutterbie 1979, Nemecek 1980, Hubbs 1985). The ovarian weight to body weight of Wisconsin banded darters average 13% from April to July with a range of 9% to 19% (Lutterbie 1979) and average 13% in New York with a peak of 29% in one individual in May (Nemecek 1980). The number of ripe ova (1.51-1.84) range from 80 to 262 (Erickson 1977).

All age I *E. lynceum* of greater than 27 mm SL were sexually mature with the reproductive season lasting from April to June. The peak percentage for ovarian weight to body weight was in April (12%) and slowly decreased until July. Brighteye darters probably have multiple spawns during the three-month period. Some individuals may have spawned later as indicated by Burr and Mayden's (1979) observation of ripe females in July 1978 in

Table 1. Percent frequency of occurrence of food items in brighteye darters from Terrapin Creek, 1983.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Total Number	30	34	40	18	19	15	41	42	33	21	25	30
Number empty	11	4	2	1	2	0	17	4	3	2	11	12
Nematoda					5.9							
Copepoda									3.3			
Diptera												
Chironomidae	89.5	96.7	100.0	100.0	70.6	93.3	87.75	71.1	86.7	68.4	78.6	77.8
Simuliidae		3.3		35.3	23.5	86.7	8.3	13.1			7.1	
Tabanidae								2.6				
Plecoptera	31.6	6.7										11.1
Ephermeroptera		3.3	26.3	47.1	35.3	6.7	8.3	65.8	40.0	63.2	21.4	27.8
Trichoptera		13.3	10.5				50.0	36.8	6.7		35.7	11.1
Orthroptera			2.6									
Undet. insects	5.3	3.3	7.9				4.2			10.5		
Fish Eggs			2.6	5.9			4.2					

Table 2. Percent volume of food organisms in brigheye darters from Terrapin Creek, 1983.

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
Total Number	30	34	40	18	19	15	41	42	33	21	25	30
Number empty	11	4	2	1	2	0	17	4	3	2	11	12
Nematoda					0.3							
Copepoda									*			
Diptera												
Chironomidae	55.2	80.6	86.7	51.6	44.8	24.3	48.6	42.6	56.1	39.3	36.3	64.4
Simuliidae		1.0		12.8	15.3	75.3	4.4	13.5			4.7	
Tabanidae								0.5				
Plecoptera	39.1	3.9										15.4
Ephermeroptera		1.1	7.4	34.9	39.6	0.4	2.2	25.1	43.3	54.6	5.6	9.6
Trichoptera		17.5	2.7				42.8	18.3	0.6		53.4	10.6
Orthroptera			0.9									
Undet. insects	5.7	0.7	1.6				1.3			6.1		
Fish Eggs			0.8	0.7			0.8					

* less than 0.01

Terrapin Creek. Fecundity ranged from 21 to 301. Spawning has not been observed.

Feeding is similar for both species of darter and chironomids are the predominant food. Simuliidae, Trichopterans and Ephermeropterans are consumed to a lesser extent by both *E. zonale* (Erickson 1977), Adamson and Wissing 1977, Bryant 1979, Cordes and Page 1980, Nemecek 1980) and *E. lynceum.* Feeding activity in banded darters in the Iroquois River, Illinois increased markedly after sunrise, peaked (in weight of stomach contents) at midday (1800 hrs), and decreased after sunset (Cordes and Page 1980). Feeding activity in brighteye darters in Terrapin Creek also increased at sunrise, decreased later in the morning, peaked at 1700 hrs, and ceased after sunset.

LITERATURE CITED

Adamson, S.W., and T.E. Wissing. 1977. Food habits and feeding periodicity of the rainbow, fantail, and banded darters in Four Mile Creek. Ohio J. Sci. 77:164-169.

Braasch, M.E., and P.W. Smith. 1967. The life history of the slough darter, *Etheostoma gracile* (Pisces: Percidae). Ill. Nat. Hist. Surv. Biol. Notes No. 58. 12 p.

Bryant, R. T. 1979. The life history and comparative ecology of the sharphead darter, *Etheostoma acuticeps.* Unpub. M.S. Thesis, Univ. Tennessee.

Burr, B.M., and R.L. Mayden. 1979. Records of fishes in Western Kentucky with additions to the known fauna. Trans. Ky. Acad. Sci 40:58-67.

Burr, B. M., and M.L. Warren, Jr. 1986. A distribution atlas of Kentucky fishes. Kentucky Nature Preserves Commission. Scientific and Technical Series Number 4. 398 p.

Cross, F.B. 1967. Handbook of the fishes of Kansas. Misc. Publ. Mus. Nat. Hist., Univ. Kansas. 45 p.

Cordes, L.E., and L.M. Page. 1980. Feeding chronology and diet composition of two darters (Percidae) in the Iroquois River System, Illinois. Amer. Midl. Nat. 104:202-206.

Erickson, J.E. 1977. The life history of the banded darter, *Etheostoma zonale* (Cope), in the Cannon River, Minnesota. Unpubl. Ph.D. Thesis, Univ. Minn.

Etnier, D.A. and W. C. Starnes. 1986. *Etheostoma lynceum* removed from the synonomy of *Etheostoma zonale* (Pisces, Percidae). Copeia 1986:832-836.

Hannan, R.R., M.L. Warren, Jr., K.E. Camburn, and R.R. Cicerello. 1982. Recommendations for Kentucky's outstanding resource waters with water quality criteria for protection. Kentucky Nature Preserves Commission, Technical Report. Frankfort, KY.

Harvey, B.C. 1987. Susceptibility of young-of-the-year fishes to downstream displacement by flooding. Trans. Amer. Fish. Soc. 116:851-855.

Holbrook, W.P., and D.C. Tarter. 1977. Some aspects of reproduction in the eastern banded darter, *Etheostoma zonale zonale* (Cope) in a West Virginia stream. Sci. Bio. J. 1977:418-426.

Hubbs, C. 1985. Darter reproductive seasons. Copeia 1985:56-69.

John, K.R. 1964. Survival of fish in intermittent streams of the Chiricahua Mountains, Arizona. Ecology 45:112-119.

Lachner, E.A., E.F. Westlake, and P.S. Handwerk. 1950. Studies on the biology of some percid fishes from western Pennsylvania. Amer. Midl. Nat. 43:92-111.

Leslie, P. H., and D.H.S. Davis. 1939. An attempt to determine the absolute number of rats on a given area. J. Animal Ecol. 8:94-113.

Lutterbie, G.W. 1977. Reproduction and age and growth in Wisconsin darters. Reports on the Fauna and Flora of Wisconsin No. 15. The Museum of Natural History. Steven's Point, Wisconsin. 43 p.

Matthews, W. J. 1986. Fish faunal structure in an Ozark stream:

stability, persistence and a catastrophic flood. Copeia 1986:388-397.

May, B. 1969. Observations on the biology of the variegated darter, *Etheostoma variatum* (Kirtland). Ohio J. Sci. 69:85-92.

Miller, R. J., and H.W. Robinson. 1973. The Fishes of Oklahoma. Oklahoma State University Press.

Nemecek, R. J. 1980. The comparative ecology of three species of darters in the genus *Etheostoma: Etheostoma variatum* (Kirtland), *Etheostoma caeruleum* (Storer), and *Etheostoma zonale* (Cope) in the Allegheny River Drainage of Western New York. Unpubl. Ph.D. Thesis. St. Bonaventure Univ.

New, J.G. 1966. Reproductive behavior of the shield darter, *Percina peltata*, in New York. Copeia 1966:20-28.

Pickford, G.E. and J.W. Atz. 1957. The physiology of the pituitary gland of fishes. New York Zoological Society, 613 p.

Ryon, M.G. 1986. The life history and ecology of *Etheostoma trisella* (Pisces:Percidae). Amer. Midl. Nat. 115:73-86.

Schwartz, F. J. 1965. Densities and ecology of the darters of the Upper Allegheny River Watershed. Pymatuning Lab. Ecolog., Univ. Pittsburgh, Spec. Publ. 3:95-103.

Seesock, W.C. 1979. Some aspects of the life history and ecology of the coldwater darter, *Etheostoma ditrema*, from Glencoe Spring, Etowah County, Alabama. Unpubl. M.S. Thesis. Auburn University.

Taber, C.A., and B.A. Taber. 1983. Reproductive biology and age and growth of the Missouri saddled darter, *Etheostoma tetrazonum*. Amer. Midl. Nat. 109:222-229.

Tsai, C., and E. C. Raney. 1974. Systematics of the banded darter *Etheostoma zonale* (Pisces:Percidae). Copeia 1977:1-24.

Windell, J.T. 1971. Food analysis and rate of digestion. Pages 214-226, *in* W.E. Ricker (ed.), Methods for assessment of fish production in fresh waters. Second ed. Blackwell Scientific Publications, Oxford.