

Spawning Behavior in Seven
Species of Darters (Pisces: Percidae)

LAWRENCE M. PAGE AND MICHAEL E. RETZER

Illinois Natural History Survey,
607 E. Peabody, Champaign, Illinois 61820

AND

ROBERT A. STILES

Department of Biology,
Samford University, Birmingham, Alabama 35209

ABSTRACT.— Recent observations reveal that *Percina evides* is an egg-burier, *Etheostoma duryi*, *E. asprigene*, and *E. chlorosomum* are egg-attachers, *E. aquali* and *E. microlepidum* are egg-clumpers, and *E. barbouri* is an egg-clusterer. *Etheostoma duryi* attaches its eggs to rocks; *E. asprigene* and *E. chlorosomum* attach their eggs to plants. With documentation of egg-clumping in *E. aquali* and *E. microlepidum*, three species of the subgenus *Nothonotus* now are known to be egg-clumpers and three to be egg-buriers. Sites of egg-deposition are known for 57 species of darters.

Darters spawn in four general ways: (1) they bury their eggs in the substrate and abandon them, (2) attach them over a relatively large area to objects (usually plants or rocks) above the substrate and abandon them, (3) clump them in the interface between a slanted stone and the stream substrate and guard them until they hatch, or (4) cluster them on the underside of an object (stone or log) and guard them until they hatch. Winn (1958) discussed these modes of behavior in darters. Page (in press) summarizes information on 48 species for which spawning behavior or at least the site of egg deposition had been reported in the literature. Page et al. (1981) provided data on spawning in two additional species — *Etheostoma longimanum* Jordan and *Etheostoma obeyense* Kirsch, and O'Neil (1981) on a third species — *Etheostoma coosae* (Fowler). Herein are presented data on six more species — *Percina evides* (Jordan and Copeland), *Etheostoma duryi* Henshall, *Etheostoma asprigene* (Forbes), *Etheostoma barbouri* Kuehne and Small, *Etheostoma aquali* Williams and Etnier, and *Etheostoma microlepidum* Raney and Zorach — and more detailed information on *Etheostoma chlorosomum* (Hay). All species of darters for which the site of egg deposition now is known are categorized in Table 1.

Percina (Ericosma) evides. — As are all species of *Percina* reported to date (Table 1), *P. evides* is an egg-burier. On 9 July 1971, 2 June 1972, and 17 June 1979, at water temperatures of 20°, 17°, and 18° C, respectively, pairs of *P. evides* were observed spawning in Little River, Blount County, Tennessee. All spawnings occurred over sand and gravel interspersed with cobble and boulders in water 30 to 60 cm deep in the upper parts of riffles. Current readings, taken on the bottom with a Teledyne Gurley Pygmy Current Meter, were 0.20 to 0.61 m/ sec.

Table 1. Species in each of four categories of darter spawning behavior. References given in text or by Page (in press).

BURIERS	ATTACHERS	CLUMPERS	CLUSTERERS
<i>Percina (Alvordius) maculata</i>	<i>E. (Etheostoma) blennioides</i>	<i>E. (Nothonotus) maculatum</i>	<i>E. (Boleosoma) nigrum</i>
<i>P. (A.) peliata</i>	<i>E. (Nanostoma) zonale</i>	<i>E. (N.) microlepidum</i>	<i>E. (B.) olmstedii</i>
<i>P. (A.) notogramma</i>	<i>E. (N.) coosae</i>	<i>E. (N.) aquali</i>	<i>E. (B.) perlongum</i>
<i>P. (Ericosma) evides</i>	<i>E. (N.) simoterum</i>		<i>E. (B.) longimanum</i>
<i>P. (Hypohomus) aurantiaca</i>	<i>E. (N.) duryi</i>		<i>E. (Catonotus) olivaceum</i>
<i>P. (Cottogaster) copelandi</i>	<i>E. (N.) barrenense</i>		<i>E. (C.) squamiceps</i>
<i>P. (Percina) caprodes</i>	<i>E. (N.) rafinesquei</i>		<i>E. (C.) neopterum</i>
<i>Etheostoma (Litocara) nianguae</i>	<i>E. (Ia) vitreum</i>		<i>E. (C.) kennicotti</i>
<i>E. (Etheostoma) tetrazonum</i>	<i>E. (Vaillantia) chlorosomum</i>		<i>E. (C.) flabellare</i>
<i>E. (E.) variatum</i>	<i>E. (Belophlox) okaloosae</i>		<i>E. (C.) virgatum</i>
<i>E. (Doration) stigmaeum</i>	<i>E. (Villora) edwini</i>		<i>E. (C.) obeyense</i>
<i>E. (Nothonotus) rufilineatum</i>	<i>E. (Ozarka) boschungii</i>		<i>E. (C.) barbouri</i>
<i>E. (N.) camurum</i>	<i>E. (O.) trisella</i>		<i>E. (C.) smithi</i>
<i>E. (N.) tippecanoe</i>	<i>E. (Oligocephalus) lepidum</i>		<i>E. (C.) striatulum</i>
<i>E. (Oligocephalus) spectabile</i>	<i>E. (O.) asprigene</i>		
<i>E. (O.) caeruleum</i>	<i>E. (O.) grahami</i>		
<i>E. (O.) radiusum</i>	<i>E. (O.) ditrema</i>		
	<i>E. (Boleichthys) exile</i>		
	<i>E. (B.) fusiforme</i>		
	<i>E. (B.) gracile</i>		
	<i>E. (B.) proeliare</i>		
	<i>E. (B.) fonticola</i>		
	<i>E. (B.) microperca</i>		

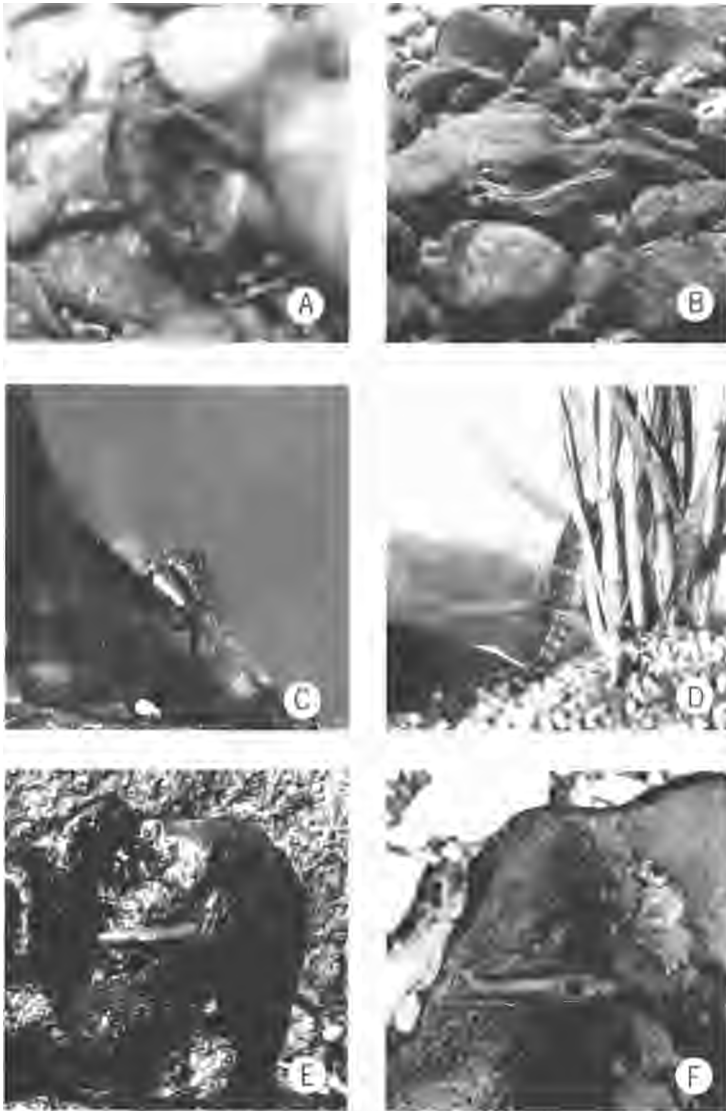


Fig. 1. Egg deposition sites of darters. A) *Percina evides* spawning in Little River, Blount Co., TN, 17 June 1979. B) *Etheostoma duryi* spawning in Butler Creek, Lawrence Co., TN, 5 April 1975. C) *Etheostoma chlorosomum* spawning in aquarium; eggs are being deposited on dead leaf. D) *E. asprigene* spawning in aquarium; eggs are being deposited on leaves of grass. E) *E. barbouri* male and his nest of eggs on the underside of stone removed from Pettys Fork, Adair Co., KY, 29 May 1981. F) *E. aquali* male and his nest of eggs on underside of stone removed from Buffalo River, Lewis Co., TN, 5 May 1981. The male *E. barbouri* and *E. aquali* were guarding the eggs prior to removal.

Prespawning activities typically consisted of a female swimming fairly rapidly over the bottom, examining the substrate to locate a spawning site, closely followed by a male. When the female stopped, the male mounted and, if the female did not swim away, vibrated his head and body. If not ready to spawn, the female swam away. Once the female selected the spawning location, vibrations of the male and female became intense, and as eggs and sperm were released the female's genital region pushed into the substrate displacing sand and gravel (Fig. 1A). Once the spawning act was completed, the female rested on the bottom for up to three minutes before seeking a new site.

Males twice were observed reversing their positions during mounting. In the first instance, the female had stopped in a sand-gravel depression among cobble with her head pointing downstream. The courting male mounted with his head over hers and vibrated several times. She quivered in response, then after about one minute he turned and positioned himself with his head upstream over her tail. They remained head-to-tail for about another minute, then the female turned to face upstream for a few seconds before returning to a head-to-tail position. The male turned to put his head over the female's, but soon returned to a head-to-tail position. The female then turned to face upstream, and head-to-head, spawned. Shortly thereafter the male was displaced by a larger male and the female moved a short distance to a new site between two rocks. The second male mounted with his head over the female's, but soon turned to a head-to-tail position. After about one minute he returned to the head-to-head position and then back to head-to-tail. The female left the area with the male in pursuit.

By aligning head-to-tail, the males appeared to have been attempting to induce the female to turn around; alternatively, by positioning his tail over the female's head, the male may have been stimulating her nape with tubercles on his anal fin. The first explanation seems to be supported by the fact that, of the four pairs of *P. evides* observed courting, only two males, courting the same female, displayed this head-to-tail maneuver. The female changed her positions, in one instance turning around to spawn facing upstream, and in the other seeking another spawning site. Additional observations may yield a more definitive explanation for head-to-tail maneuvering.

Etheostoma (Nanostoma) duryi. — *Etheostoma duryi* inhabits runs and pools of streams with moderate current and a rocky substrate. On seven dates between early March and late May, *E. duryi* was observed spawning in Butler and Factory creeks, Lauderdale County, Alabama, and Lawrence County, Tennessee. The reproductive behavior of *E. duryi* is essentially the same as that reported for the closely related *Etheostoma simotermum* (Cope) (Page and Mayden 1981). Eggs usually are deposited individually in slight depressions on the sides, or less often on the tops, of rocks.

Prior to spawning, females swam slowly over the substrate, examining the sides of rocks for sites on which to attach eggs. Typically, as a

female moved about, a male followed closely and drove away approaching males. Agonistic encounters between males usually consisted of the larger male swimming at, or making a quick dash at, the smaller male. Two males about the same size sometimes engaged in lateral displays (with median fins held erect). Females accepted any male, and if a male previously courting her was chasing away an intruding male, the female sometimes spawned with a third male.

When a female selected a spawning site, she aligned her body over it and the male mounted. Both vibrated with their bodies in an S-shaped figure and their genital papillae pressed against or near the rock (Fig. 1B). *Etheostoma duryi* appeared to vibrate less intensely than *E. simoterum*; however, verification of this will require cinematographic analysis.

Etheostoma (Vaillantia) chlorosomum. — Winn (1958), paraphrasing C. Hubbs, stated that in Texas *E. chlorosomum* lays its eggs on plants or plant debris, but gave no other details. Three breeding male and three ripe female *E. chlorosomum*, 40 to 50 mm SL, were captured in East Fork Kaskaskia River, Marion County, Illinois, on 30 April 1981 in a sand-bottom pool at 22° C and a maximum depth of 80 cm. At one end of the pool was a large accumulation of logs and other plant debris. East Fork is a fairly slow stream composed mostly of long pools but with some gravel-bottom riffles.

The *E. chlorosomum* were transferred at 0900 hr the following day to a 40 l aquarium (23° C) at the Illinois Natural History Survey (INHS). One half of the aquarium bottom was covered with sand, the other half with gravel. In one corner a large stone was propped on a smaller stone so that its underside was accessible for egg-clustering or clumping, and its top and sides were available for egg-attachment. A small log (5 cm diameter) was placed across the aquarium, over the sand and gravel, for attachment of eggs. An accumulation of filamentous algae, dead leaves, and twigs was provided at the end of the log over sand.

Little activity ensued until 1145 hr when the darters were fed live cladocerans. After feeding, the males became aggressive towards one another and courted the females. Both aggressive and courting behavior consisted mainly of lateral displays. Usually when displaying, the males were swimming and quivering about 1 cm above the substrate. All such activities occurred over the sand-covered half of the aquarium.

At 1230 hr, one male succeeded in chasing the other two out of the sand-covered part of the aquarium and sequentially enticed all three females to spawn. Spawning continued until 1700 hr when observations were discontinued. As in other egg-attaching darters, the female selected the site of egg-deposition, the male closely followed her to the site and mounted her, the pair vibrated, and eggs and sperm were released. Often the male mounted a female while she remained horizontal on the substrate and beat her with his pectoral fins until she swam into the plant material. Usually 1 to 3 eggs (1 mm diameter) were laid at a time,

and all were attached to plant material. Most were deposited on a twig (3 mm diameter), but others were laid in the algae or on dead leaves (Fig. 1C), and a few were laid on the log.

Etheostoma (Oligocephalus) asprigene. — Five breeding (2 males, 3 females) *E. asprigene*, 35 to 50 mm SL, were captured in Cane Creek (Saline system), Gallatin County, Illinois, on 9 April 1981 in fairly fast water just below an artificial riffle (of rip-rap) in 20° C water. For much of its length Cane Creek is a sluggish stream with clay and sand substrates. At 0900 hr the following day the darters were transferred to a 40 l aquarium at INHS. Because the darters were captured over gravel in current, and because some consubgenerics of *E. asprigene* (*Etheostoma spectabile* (Agassiz) and *Etheostoma caeruleum* Storer) bury their eggs in gravel, the substrate provided in the aquarium was fine gravel. Two large stones, one propped on one end to create a space beneath, were also placed in the aquarium to provide the opportunity for attachment of the eggs to their sides or to cluster or clump them on the underside.

By 1000 hr the males were courting the females, and by 1200 hr one pair was spawning. Eggs were attached, 1 to 3 at a time, 15 to 25 cm above the substrate, to the glass in the black corners of the metal-frame aquarium. We assumed that the vertical position of the corner posts of the aquarium simulated to the darters vertical shafts of vegetation, and at 1300 hr a crabgrass plant (no aquatic vegetation was immediately available) was rooted in the gravel. Spawning continued to be restricted to the corners of the aquarium until about 1600 hr, and then one pair moved to the crabgrass and began laying eggs on its blades (Fig. 1D). Once spawning on the grass began, no more eggs were laid in the corners of the aquarium. Spawning continued for several hours, but ended that day. Only one of the two males spawned, but with at least two of the three females.

The spawning act in *E. asprigene* occurred as described above for *E. chlorosomum*. Although both crabgrass and aquarium corners are artificial spawning substrates, it is apparent from the aquarium observations that *E. asprigene* is an egg-attaching species. Eggs were not buried in the substrate, or clustered or clumped on the underside of the available stone. The fact that eggs were not laid on the tops or sides of the large stones suggests that in nature eggs are attached to living or dead plant material. Other species of the subgenus *Oligocephalus* that lay their eggs on plants are *Etheostoma lepidum* (Baird and Girard), *Etheostoma grahmi* (Girard), and *Etheostoma ditrema* Ramsey and Suttkus (Strawn 1956; Winn 1958; Seesock et al. 1978).

Etheostoma (Catonotus) barbouri. — Two nests of *E. barbouri* eggs were found on the undersides of flat stones in a large slab-rock pool in Pettys Fork (of Russell Creek), Adair County, Kentucky, on 29 May 1981. The first nest, found in water about 50 cm deep, contained 70 eggs (2.1 mm diameter) and was guarded by a breeding male (Fig. 1E). The second nest was found on a stone dragged up in a minnow

seine and contained 42 eggs. *E. barbouri* is the last of the ten taxonomically described species of *Catonotus* to be confirmed as an egg-clustering species.

Etheostoma (Nothonotus) aquali. — The subgenus *Nothonotus* of *Etheostoma* is the only subgenus of darters in which some species bury their eggs and others clump them (Table 1). From a study conducted in Pennsylvania, Raney and Lachner (1939) first reported the egg-deposition site of *Etheostoma maculatum* Kirtland. In Tennessee, Stiles (1972) found eggs of *E. maculatum* on the undersides of stones held as territories by males. To date, no other species of *Nothonotus* had been reported as an egg-clumper.

On 5 May 1981 we found four nests of *E. aquali* in a large rubble riffle in Buffalo River, Lewis County, Tennessee. The water was swift, 22° C, and averaged 30 cm deep where the nests were found. Eggs were difficult to find in the swift water, and it was even more difficult to capture the male in association with the nest. However, one 63 mm SL male was captured beneath a stone to which a clump of eggs was attached. (Fig. 1F).

Nests of *E. aquali* were similar in construction to those of *E. maculatum* as described by Raney and Lachner (1939). Unlike the single-layer clusters of species of the subgenera *Boleosoma* and *Catonotus*, nests of *E. maculatum* and *E. aquali* contain a multi-layer clump of eggs. Each nest contained eggs in various stages of development, which obviously were the results of more than one spawn. One nest, removed and preserved for an accurate egg count, contained 551 eggs averaging 1.8 mm in diameter.

Two male and four female *E. aquali*, 50 to 65 mm SL, were collected in Buffalo River on 5 May 1981 and returned to INHS. On 8 May they were placed in an 80 l aquarium, at 24° C, outfitted with a current pump. Two stones were propped up the undersides accessible as nesting sites. Observations were made through the next two days but no spawning activities were seen. However, by 0800 hr on 11 May a male had established a territory under the smaller of the two stones (the other male had died) and was guarding three small clumps of eggs. The clumps were separated by distances of at least 2 cm, but all were in the interface between the nest stone and the gravel substrate. No further spawning occurred.

The only notable behavior of aquarium-held *E. aquali*, other than the constant attention given his territory by the breeding male, was that of the females. On two occasions a female was seen to swim beneath the nest stone and tightly wedge herself (more or less right-side up) in the interface between the stone and gravel substrate. Although the male ignored her, it appears that eggs are laid with the female wedged

between the rock and substrate. One of us (RAS) has seen similar behavior in *E. maculatum* in the upper Tennessee River system. The clumping of eggs results not from the stacking of eggs on top of one another, but because the eggs are pumped into the interface between the slanted stone and stream substrate. When the stone is lifted from the water, the adhesive clump (or at least part of it) is attached.

Although most of the *E. aquali* eggs laid in the aquarium died, six of a clump transferred to an aerated 600 ml glass dish hatched. Hatching time was three to four days at a fluctuating 24 to 28° C. Hatchlings were 6.5 mm TL, had well-developed pectoral fins and jaws, and a mid-dorsal series of bright gold flecks.

Etheostoma (Nothotus) microlepidum. — One nest of *E. microlepidum* eggs and an attendant male, 53 mm SL, were found in a moderately fast riffle in East Fork Stones River, Rutherford County, Tennessee, on 6 May 1981. The riffle averaged 15 cm deep and was composed of large gravel and small rubble; water temperature was 21° C. The nest contained an estimated 346 eggs, averaging 2.0 mm in diameter, arranged in a multi-layer clump essentially identical to those of *E. maculatum* and *E. aquali*.

Etheostoma maculatum, *E. aquali*, and *E. microlepidum* are closely related, and we predicted that all would be egg-clumpers. Relationships among other species of *Nothotus* are less obvious, and it is difficult to predict which clump eggs and which bury eggs. According to Zorach (1972), other relatives of *E. maculatum* are *Etheostoma acuticeps* Bailey, *Etheostoma moorei* Raney and Suttkus, and *Etheostoma rubrum* Raney and Suttkus; confirmation of egg-clumping (the derived state) in these species would confirm their recent shared ancestry with *E. maculatum*.

Although three unrelated subgenera (i.e. nonsister-groups) of darters amass and guard their eggs, the manner in which this is accomplished in *Nothotus* is unlike that in *Boleosoma* and *Catonotus*. Among North American freshwater fishes, single-layer clusters are laid by *Boleosoma*, *Catonotus*, and the minnow genus *Pimephales* (McMillan and Smith 1974); multi-layer clumps of eggs are laid by *Nothotus*, *Noturus* (madtoms) (Mayden and Burr 1981), and some *Cottus* (sculpins) (Smith 1922). The selective factors separating these two types of behavior remain to be determined.

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LITERATURE CITED

- Mayden, Richard L., and B. M. Burr. 1981. Life history of the slender madtom, *Noturus exilis*, in southern Illinois (Pisces: Ictaluridae). Occas. Pap. Mus. Nat. Hist. Univ. Kans. 93:1-64.
- McMillan, Victoria E., and R. J. F. Smith. 1974. Agonistic and reproductive behavior of the fathead minnow (*Pimephales promelas* Rafinesque). Z. Tierpsychol. 34:25-58.
- O'Neil, Patrick E. 1981. Life history of *Etheostoma coosae* (Pisces: Percidae) in Barbaree Creek, Alabama. Tulane Stud. Zool. Bot. 23(1):75-83.
- Page, Lawrence M. In press. Handbook of Darters. T.F.H., Inc., Neptune, NJ.
- _____, and R. L. Mayden. 1981. The life history of the Tennessee snubnose darter, *Etheostoma simoterum* in Brush Creek, Tennessee. Ill. Nat. Hist. Surv. Biol. Notes 117. 11 pp.
- _____, W. L. Keller and L. E. Cordes. 1981. *Etheostoma (Boleosoma) longimanum* and *E. (Catonotus) obeyense*, two more darters confirmed as egg-clusterers. Trans. Ky. Acad. Sci. 41:35-36.
- Raney, Edward C., and E. A. Lachner. 1939. Observations on the life history of the spotted darter, *Poeciliichthys maculatus* (Kirtland). Copeia 1939(3): 157-165.
- Seesock, Wendy E., J. S. Ramsey and F. L. Seesock. 1978. Life and limitation of the goldwater darter (*Etheostoma ditrema*) in Glencoe Spring, Alabama. ASB (Assoc. Southeast. Biol.) Bull. 25:56.
- Smith, Bertram G. 1922. Notes on the nesting habits of *Coitus*. Pap. Mich. Acad. Sci. Arts Lett. 2:222-224.
- Stiles, Robert A. 1972. The comparative ecology of three species of *Nothonotus* (Percidae — *Etheostoma*) in Tennessee's Little River. Unpubl. Ph.D. Dissert., Univ. Tennessee, Knoxville. 97 pp.
- Strawn, Kirk. 1956. A method of breeding and raising three Texas darters. Part II. Aquarium J. 27:12-14, 17, 31-32.
- Winn, Howard E. 1958. Comparative reproductive behavior and ecology of fourteen species of darters (Pisces-Percidae). Ecol. Monogr. 28:155-191.
- Zorach, Timothy. 1972. Systematics of the percid fishes, *Etheostoma camurum* and *E. chlorobranchium* new species, with a discussion of the subgenus *Nothonotus*. Copeia 1972(3):427-447.

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