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Darter Reproductive Seasons

Clark Hubbs

Twenty-nine darters have reproductive intervals demonstrated and geographic variation is shown for three species based on ten or more populations. The data from most populations are in accord with an hypothesis of multiple spawning by individual females.

The length of darter reproductive seasons varies with latitude. Populations from the southern United States breed over longer intervals than those from more northern locations. Most of the difference is based on earlier initiation in southern than in northern regions; whereas, the end of the breeding season tends to be similar at different latitudes. The spawning season is longer in stenothermal habitats than it is in eurythermal habitats (of various latitudes). The data are in accord with hypotheses that photoperiod plays a major role in reproductive initiation and temperature is important in reproductive termination.

Reproductive seasons have been ascertained for many darters (Page, 1983; Kuehne and Barbour, 1983); however, most reports relate to observations of spawning occurrence during collection intervals with few repeated efforts. Although Page (1983) opined that only one clutch was produced each season, my data suggest long reproductive seasons with multiple spawnings (Hubbs, 1983). Additionally, Gale and Deutsch (1985) provide data demonstrating multiple spawnings for *Etheostoma olmstedi* in Pennsylvania. My opinion that most darters have multiple clutches has been expressed in several papers but the data base has been presented in detail only in Hubbs and Strawn (1957a) who showed that groups of ova sequentially differentiated from the pool of immature ova. Herein, I report known dates of reproduction for several populations of three darters and for one or more populations of 26 additional species. Those data are in general agreement with "Natural History" data presented by Page (1983) and Kuehne and Barbour (1983) except that my information often substantially extends the previously reported reproductive seasons.

Materials and Methods

The data reported here are derived primarily from my previous hybridization experiments (Hubbs, 1967). The procedures were to obtain darters from a variety of geographic locations and return them to Austin. The stocks were maintained without feeding at ca 15 C. Females with clear, translucent eggs were considered to be ripe and used for hybridization (or control) experiments. During most experiments some eggs developed embryos that hatched into successful larvae; therefore, this conservative measure of reproduction is used here. Only those females whose eggs were fertilized are reported. If I were to use clear, translucent eggs as the index for reproduction, an occasional additional reproductive day would have been reported (especially for species that were tested infrequently and their reproductive criteria not as well understood). Females held under those laboratory conditions ceased producing eggs in 4 to 5 days after 50 to 90% of them had ovulated. Consequently, it is apparent that at least half, and presumably all, females were in reproductive cycle at the times of capture. Samples early or late in the reproductive seasons reported here or of poorly understood species may have had smaller fractions of females reproductive, but this occurred in fewer than 1% of the samples. For the data reported here female capture was up to five days prior to the recorded date. Each date is considered as a datum even though that date may have been represented by 50 ripe females on each of three separate years. Each year had similar reproductive seasons, thus pooling of years did not distort the data base.

The data are for known occurrence of ripe females; it is presumed that females in natural populations were equally ripe at additional intermediate dates as all samples from within the appropriate reproductive seasons had numerous reproductive females. The data reported are for occurrence of reproductive females, thus the seasons recorded may be shorter than those that occur in nature as some females may have been reproductive before and/or after those dates recorded in my data.

The localities reported here are the same as those reported in Hubbs (1967). Commonly, adjacent localities are pooled. Most sampling was from the years 1954 through 1967. As several leap years occurred within that time frame, Feb. is considered to have 29 days.

Etheostoma lepidum

The greenthroat darter reproductive season has been reported as Oct. or Nov. through May with populations in stenothermal environments having a longer spawning season than those in more eurythermal environments (Hubbs and Strawn, 1957a). These data reported here (Fig. 1) corroborate that report. It should be noted that the more stenothermal environments (S. Concho, Mt. Home, S. Guadalupe) have longer recorded reproductive seasons than the more eurythermal extensively collected environments (Hunt, Ingram, Junction). The greenthroat darter is basically a springrun species. Thus, it is scarce or absent from very eurythermal locations. Collectively (all populations pooled) greenthroat darter eggs are shown to have been fertilized on 178 of 181 days in Nov. through April (the exceptions are 20 Feb., 31 March, 25 April). Thus the species is intensively reproductive for six months and reproduction is also recorded for Sept., Oct., May and June, or at least some level of reproduction demonstrated for 10 months. Additionally, I record translucent eggs from females obtained in Blue Spring, New Mexico, in Aug. 1983; Hubbs and Strawn (1957a) recorded breeding females (based on translucent eggs) in July.

At the South Guadalupe locality, greenthroat darter females were reported to be reproductive in June, July and Aug. (Hubbs and Strawn, 1957a) (the present report records fertilized eggs from that locality in the other nine months). That paper also reported spawning (the number of eggs spawned was equivalent to the number of ripe eggs in dissected females) in the laboratory (with densities equivalent to those on

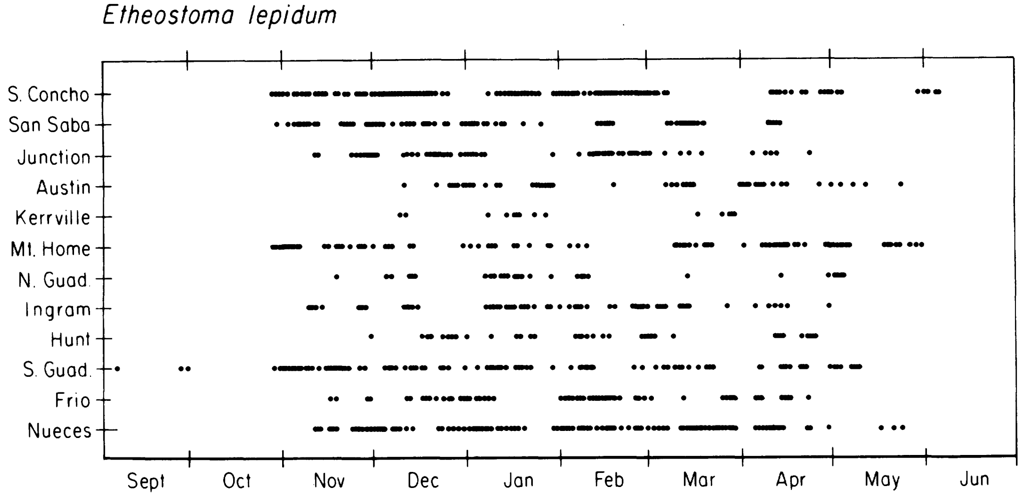

Fig. 1. Known reproductive dates for *Etheostoma lepidum* from 12 regions.

spawning riffles) every 4.9 days at 19.6 C and every 4.8 days at 20.4 C [the average temperature of central Texas springs is ca 20 C (Hubbs, 1971)]. As Hubbs and Martin (1965) showed that greenthroat darter females lay eggs primarily in daylight, it is assumed that the clutches in nature occur every five days (previous averages rounded to 5 days as nocturnal spawnings unlikely). A female from the South Guadalupe would lay 52 clutches per year based on the known interval of fertilized eggs or 73 clutches based on observations of translucent eggs. The egg volume approximates 7% of female volume. If we use a conservative figure of 5% of female volume, the summed annual contributions are 260 and 365% of female volume.

Etheostoma spectabile

The orangethroat darter has a recorded reproductive season in central Texas that is very similar to that for the greenthroat darter. The major difference is that orangethroat darters occupy more eurythermal environments, thus lack the year-round reproduction that prevails for greenthroats occupying springruns (Fig. 2). For example at Junction both species are first recorded as reproductive on 12 Nov. In general, reproduction is recorded over longer intervals for the stations at which that species is more abundant (North Guadalupe, Hunt, Kerrville, Austin for orangethroats) (S. Concho, Ingram for greenthroats). Relatively rare species are seldom collected and thus seldom recorded as ripe. The data reported here parallel those previously reported for the same species in Texas by Hubbs (1961) and by Hubbs et al. (1968). They do extend the initiation of reproduction into late Oct. Marsh (1980) has shown that the termination of spawning may be delayed until July in artificially cool hypolimnetic release waters in the Guadalupe River downstream from Canyon Reservoir. The natural reproductive season in Texas would thus be seven months with a seminatural nine-month season. Assuming a five-day interbrood interval this would mean 42 to 54 spawns per year.

The reproductive season in Arkansas extends from mid-Feb. to early June, and in Missouri from early April to early June (Fig. 2). This latter period is in accord with a March through May reproductive season in Kansas (Cross, 1967) and Missouri (Pflieger, 1975) but suggests my first Missouri samples were well after the first spawning. The Arkansas season corresponds with or is slightly longer than that of late Feb. or March to May reported by Miller and Robison (1973) for Oklahoma. The Arkansas pattern occurs in both the White River (*E. s. spectabile*) and Illinois River (*E. s. pulchellum*) tributaries (contrast White R. and Clear Cr.).

The spawning season of orangethroat darters varies with latitude. In the south, it extends for seven months, farther north (Arkansas) it lasts almost four months, yet farther north (Missouri) it lasts three months and toward the

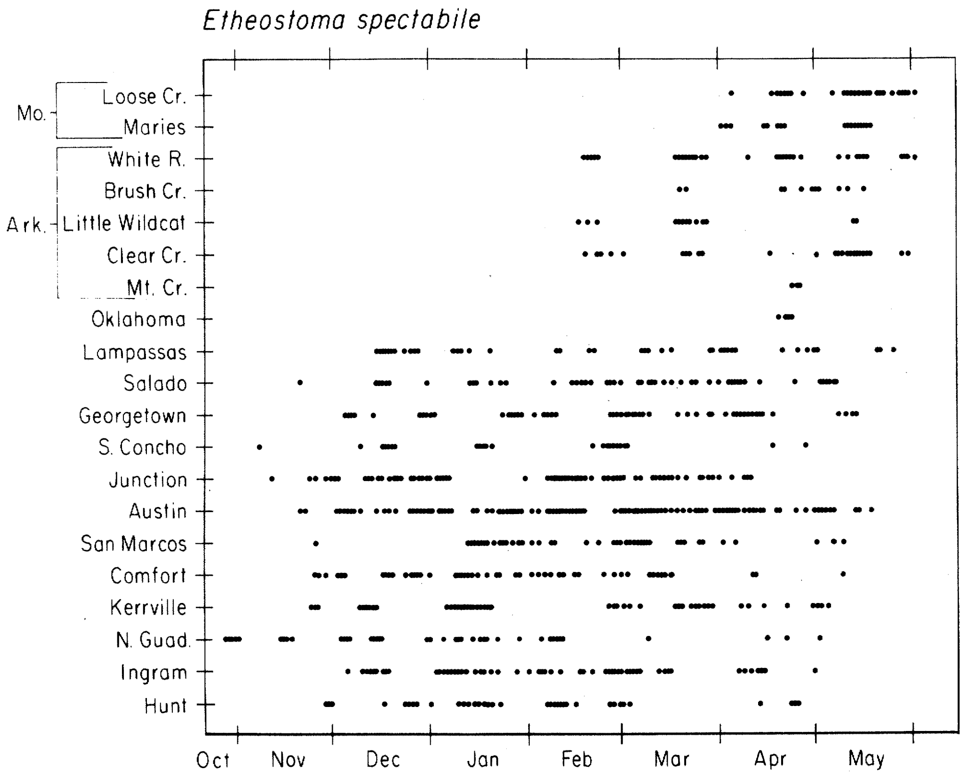

Fig. 2. Known reproductive dates for *Etheostoma spectabile* from 20 regions.

northern limit (Michigan) two months [early April to early June (Winn, 1958)]. Winn's report of peak reproduction in Kentucky and Tennessee during the first week in April corresponds better with the Missouri–Kansas season than with that of Michigan. The majority of the north–south difference in breeding season lies in the initiation [Oct. (Texas) to April (Michigan)] rather than the end [mid-May (Texas) to early June (Arkansas–Missouri–Michigan)]. Assuming equivalent interbrood intervals and equivalent individual clutch numbers in equal-sized females, Michigan females would have to survive 3.5 spawning seasons to produce the same number of offspring as Texas females would produce in one year.

Percina caprodes

The logperch has been considered to represent two species (the southern *P. carbonaria* and the northern *P. caprodes*) by Thompson (1978), an action endorsed by Morris and Page (1981), and Page (1983) but not by Kuehne and Barbour (1983). My Texas stocks would be *P. carbonaria* and my Oklahoma, Arkansas and Missouri stocks *P. caprodes* if the two taxa are considered distinct species.

The Texas stocks have been recorded as breeding from Jan. through June (Hubbs, 1961) and Oct. and Nov. (Stevenson, 1971). The latter report relates to spawning migrations and presumably involves a prespawning migration and not actual spawning. The locality referenced by Stevenson is in the Kerrville locality included in Fig. 3. That locality has a recorded breeding season of Jan. through May (presumably also late Dec.) but definitely not including Nov. during which month many logperch were examined at the same time that orangethroat darter females are reproductive. The present data demonstrate that the season is mid-Dec. to mid-May.

The logperch is commonly found in the same streams as the orangethroat darter. The two species tend to partition riffles with logperch in the deeper water or associated with larger rocks than the orangethroat darter. Nevertheless the

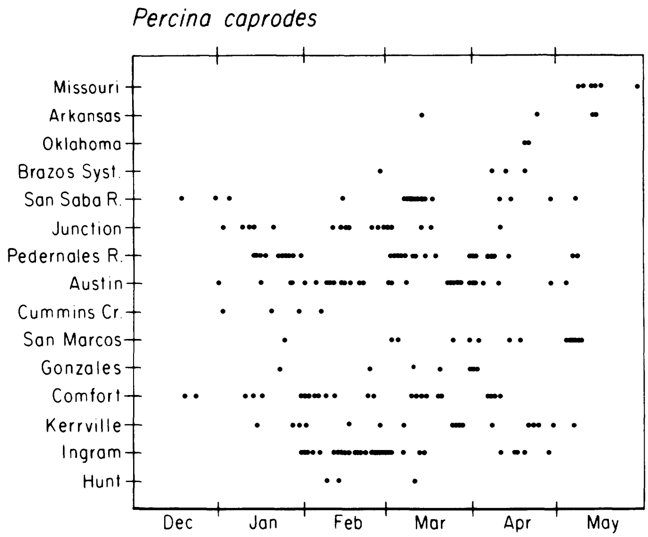

Fig. 3. Known reproductive dates for *Percina caprodes* from 15 regions.

two species are commonly taken in the same seine haul. Therefore, logperch females were available for examination for ripe eggs on most of those dates orangethroat darters were examined. Both species had numerous reproductive individuals at five localities (Ingram, Kerrville, Comfort, Austin, Junction). At each locality orangethroat darters were reproductive before logperch (+56, +52, +24, +41 and +52 days, respectively, $\bar{x}$ = 45 days earlier), but the data on last reproduction are more equivocal (−3, +7, −29, −14, 0, $\bar{x}$ = 8 days later). The obvious conclusion is that the breeding season for logperch starts later but ends at about the same time as that for orangethroat darters in central Texas. That season would be mid-Dec. or early Jan. to mid-May. In a similar fashion, the reproductive season for logperch in Arkansas and Missouri starts later but ends at about the same date as that of orangethroat darters.

The breeding season for male logperch is substantially longer than that for female logperch as various *Etheostoma* × *P. caprodes* hybrids were produced in Nov., a month before the initiation of female reproduction. This observation is in accordance with the generalization that for most fishes males are reproductive earlier (and longer) than females (Lagler et al., 1977; Nikolski, 1963).

The spawning season for female logperch in Texas is Dec. to mid-May; Arkansas, mid-March to mid-May (Miller and Robison, 1973, list late March or April for Oklahoma); Missouri, April and May (Pflieger, 1975) (my data cover only May); southern Michigan, April to late May or early June, and northern Michigan, mid-June to late July (Winn, 1958). Except for northern Michigan (where orangethroat darters do not occur) the pattern is very similar to that of orangethroat darters, progressively shorter spawning seasons with more northerly latitudes. The majority of the change is in spawning initiation and little difference in the date of the end of the reproductive season.

Miscellaneous *Percina*

Bigscale logperch.—The reproductive season for *Percina macrolepida* in its natural range has not been previously recorded. Ripe females are known to occur from 26 Feb. to 14 April [all from central Texas localities (Fig. 4)]. The occurrence of small individuals (ca 25 mm SL) in Lake Texoma in early June suggests a similar reproductive interval there. The available data on male reproduction show no additional reproductive interval.

Dusky darter.—The breeding season for *Percina sciera* has been reported as late May to early July in Illinois (Page and Smith, 1970) and Feb. to June in Texas (Hubbs, 1961). My present data slightly expand that reported two decades ago with substantial Jan. reproduction recorded. In

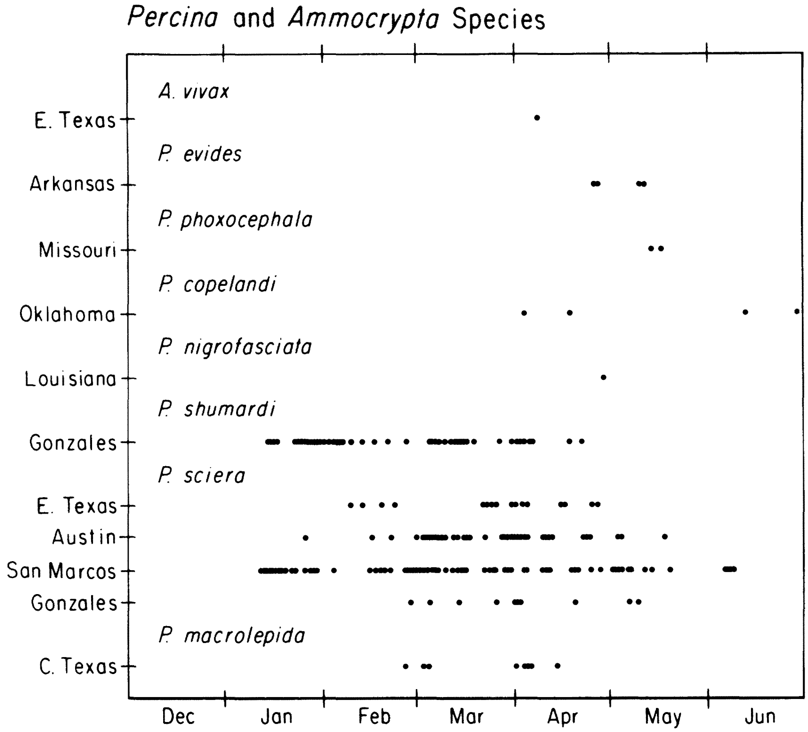

Fig. 4. Known reproductive dates for seven species of *Percina* and *Ammocrypta vivax*.

the reasonably stenothermal waters of the San Marcos River, dusky darters are known to be reproductive from 12 Jan. to 9 June (Fig. 4). Other localities (with more thermal variation) have not been shown to have reproductive individuals for such a long interval but for the most part have not been sampled as frequently.

The reproductive initiation for male dusky darters is considerably earlier than for the females recorded here. Several males from Austin had visible sperm that fertilized eggs (of *Etheostoma*) in late Dec. and early Jan. The first date was 29 Dec., or nearly a month before any females from that population have been shown to be ripe.

The reproductive interval of dusky darters in San Marcos is five months, but in Illinois Page and Smith (1970) list an interval of less than two months. Populations from all four Texas areas have known reproductive intervals of three or more months.

River darter.—The reproductive season for *Percina shumardi* has been reported to be April in Kansas (Cross, 1967), April and May in Illinois (Thomas, 1970) and possibly June or July in Manitoba (Scott and Crossman, 1973). Starnes (1977) opines that in Tennessee the river darter spawns in Feb. and March. My data apply only to one location in the Guadalupe River near Gonzales, Texas, where river darters are shown to be reproductive from 14 Jan. to 22 April, or for more than 3 months (Fig. 4). The evidence on male reproductive intervals is essentially the same as that for females.

The recorded reproductive season for river darters in Texas is longer than that for any other geographic area. Reproductive initiation is markedly earlier in the south and the end is somewhat later in the north.

Blackbanded darter.—The reproductive season for *Percina nigrofasciata* has been reported to be Feb. to April in Louisiana and early May to early June near Auburn, Alabama (Mathur, 1973). My record from eastern Louisiana on 29 April (Fig. 4) suggests that all of April is within the reproductive interval in Louisiana.

Channel darter.—The reproductive season for *Percina copelandi* has been reported as 9–23 July in northern Michigan (Winn, 1958) and April

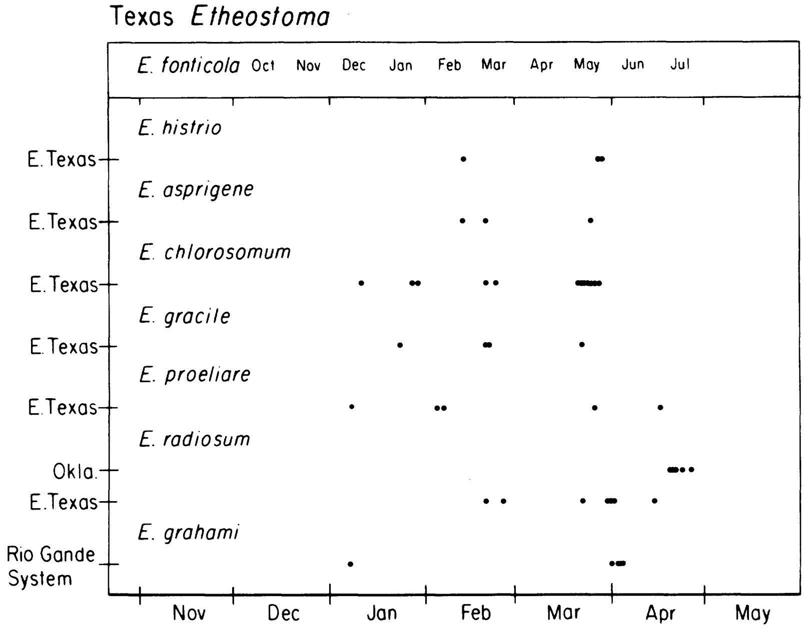

Fig. 5. Known reproductive dates for eight species of *Etheostoma* from Texas and Oklahoma. Note the data for *Etheostoma fonticola* are on a different scale.

and May in Kansas (Cross, 1967). The known reproductive season in Oklahoma extends from 4 April to 29 June (Fig. 4). The two June data points were obtained by Hubbs and Bryan (1975) from stocks obtained from the Blue River near its spring source (a stenothermal location). The breeding season in the north is substantially shorter than that in the south.

Slenderhead darter.—The reproductive season for *Percina phoxocephala* has been reported to be late May to early July in Illinois (Page and Smith, 1971) and late April into May in Missouri (Pflieger, 1975). My data for a Missouri stock are supportive of Pflieger's report (Fig. 4).

Gilt darter.—The reproductive season for *Percina evides* has been reported to be in May in Virginia (Denoncourt, 1969). Pflieger (1975) observed breeding males in late May in Missouri. I have obtained ripe females in late April and early May in Arkansas (Fig. 4).

Ammocrypta

My data relate to only one species of sand darter, *Ammocrypta vivax*. There is essentially no information on the reproductive season of the scaly sand darter. Williams (1975) noted that tuberculate males occur from mid-April to mid-Aug. My record of a ripe female in east Texas on 8 April (Fig. 4) is the only report on a female reproductive date. I also record fertilization of darter eggs by a male scaly sand darter on 5 April.

Texas/Oklahoma *Etheostoma*

Rio Grande darter.—The reproductive interval of *Etheostoma grahami* has been recorded as late March to early June (Harrell, 1980) but Strawn and Hubbs (1956) report that spawning will occur at regular intervals if the temperature remains near 20 C. My record of early Jan. ripe females (Fig. 5) is in accord with a prolonged reproductive interval in stenothermal waters. It is likely that the reproductive cycle for the Rio Grande darter is essentially the same as that of the greenthroat darter.

Orangebelly darter.—The reproductive interval for *Etheostoma radiosum* has been reported to be March through May for the Blue River, Oklahoma, by Scalet (1973). My data for Oklahoma populations are in accord with Scalet's report but in east Texas reproduction (classification based on Hubbs, 1982) extends from at least late Feb. through mid-April (Fig. 5).

Cypress darter.—The reproductive interval for *Etheostoma proeliare* has been reported to be April and May in Illinois and as early as Jan. in Louisiana (Burr and Page, 1978). My data suggest prolonged spawning from early Jan. to mid-April in east Texas (Fig. 5).

Slough darter.—The reproductive season of *Etheostoma gracile* has been reported to be March in Texas (Collette, 1962) and late May and early June in Illinois (Braasch and Smith, 1967). My data indicate the breeding season starts in Texas (east) at least by 24 Jan. (Fig. 5). The demonstrated Texas reproductive season is more than two months and that reported for Illinois is no more than a month.

Bluntnose darter.—The reproductive season of *Etheostoma chlorosomum* has been reported to be April in Kansas (Cross, 1967) and May in Illinois (Smith, 1979). My data for Texas populations demonstrate early Jan. to late March reproduction in east Texas (Fig. 5). The known spawning season in Texas populations is longer than that reported for more northern localities.

Mud darter.—Little is known of the reproductive season of *Etheostoma asprigene.* Forbes and Richardson (1908) suggested a March to May reproductive season for Illinois and Becker (1983) stated that spawning occurs in April and May at Havana, Illinois. In east Texas reproductive females are recorded from 14 Feb. to 26 March (Fig. 5).

Harlequin darter.—Little is known of the reproductive season of *Etheostoma histrio.* Kuehne and Barbour (1983) reported females apparently ready to spawn in mid-March in Mississippi and Hubbs and Pigg (1972) reported ripe females in Feb. That record is the 13 Feb. spawning recorded here (Fig. 5). Additional east Texas spawning is recorded for 28 and 29 March.

Fountain darter.—*Etheostoma fonticola* has been recorded to be reproductive in all months in San Marcos River (Strawn, 1956). Schenck and Whitesides (1977) reported apparent spawning peaks in Aug. and late winter. My data (Fig. 5) documenting fertilized eggs during 10 months (the exceptions are Aug. and Sept.) support Strawn's thesis of continuous spawning.

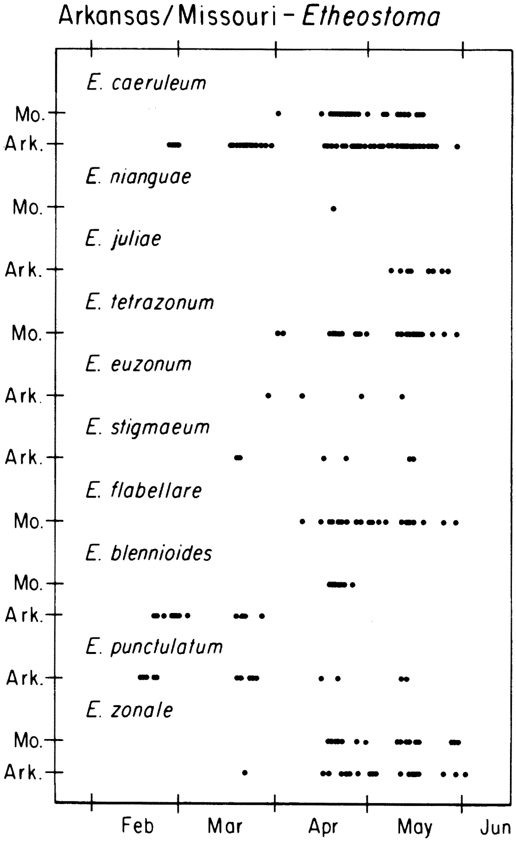

Fig. 6. Known reproductive dates for ten species of *Etheostoma* from Arkansas and Missouri.

Arkansas/Missouri *Etheostoma*

Banded darter.—The reproductive season for *Etheostoma zonale* has been reported as April and May in Oklahoma (Miller and Robison, 1973) and Kansas (Cross, 1967), April in Missouri (Pflieger, 1975) and May and June in Illinois (Forbes and Richardson, 1908) and Pennsylvania (Lachner et al., 1950). Additionally, Burr and Mayden (1979) record ripe females on 20 July in western Kentucky. My data show Arkansas reproduction from late March to early June and Missouri reproduction from mid-April to late May (Fig. 6). The longest recorded reproductive interval is for Arkansas stocks (southern).

Stippled darter.—The reproductive season for *Etheostoma punctulatum* has been reported as May (Miller and Robison, 1973), April and May with males in breeding color as late as July (Pflieger, 1975), May (Kuehne and Barbour, 1983) and probably April (Cross, 1967). My data, primarily based on a stock in a spring near Fayetteville, Arkansas, have the breeding season at least from mid-Feb. through mid-May (Fig. 6). As this species has a relatively restricted geographic range (Cloutman, 1980), it is likely that my data would apply to stenothermal waters (a preferred habitat) throughout its range.

Greenside darter.—The reproductive season for *Etheostoma blennioides* has been reported as late March and early April in Missouri (Pflieger, 1975) late April in Kentucky (Kuehne and Barbour, 1983) and April and May in Michigan (Winn, 1958). Pflieger and Winn suggested that greenside darters cease breeding earlier than other darters in Missouri, Michigan, Kentucky and Tennessee. My data support early reproduction of greenside darters with the Arkansas season in late Feb. to late March and the Missouri season in April (Fig. 6). Numerous samples of darters in both regions had reproductive females of other species but non-reproductive female *E. blennioides* throughout May.

Fantail darter.—The reproductive season for *Etheostoma flabellare* has been reported to be April to June and perhaps July (Page, 1983) at various localities. It has been recorded as April and May in Missouri (Pflieger, 1975). My data support his conclusion with reproductive females recorded on many days during those two months (Fig. 6).

Speckled darter.—The reproductive season for *Etheostoma stigmaeum* has been reported to be April in Kentucky and Tennessee (Winn, 1958), April and May in Kansas (Cross, 1967) and Missouri (Pflieger, 1975) and late March to early April in many localities (Howell, 1978). My data for Arkansas stocks suggest that the inclusive range listed for the several locations is correct (Fig. 6). I have records of ripe females from 20 March to 16 May and numerous additional records of clear eggs from females on other dates including some as late as 30 May.

Arkansas saddled darter.—The only data available on the reproductive season for *Etheostoma euzonum* are that provided by Hubbs and Strawn (1957b) on fertilized eggs obtained in May. I now have data on fertilized eggs from 30 March to 12 May (Fig. 6).

Missouri saddled darter.—The reproductive season for *Etheostoma tetrazonum* has been reported as April and May (Pflieger, 1975). My data are in accord with that season with ripe females occurring between 2 April and 30 May (Fig. 6).

Yoke darter.—The reproductive season for *Etheostoma juliae* has been reported to be in May in Missouri (Pflieger, 1975) and April to early July in Arkansas (Hill, 1968). My data based on Arkansas stocks are in accord with a late reproductive season (Fig. 6). The earliest ripe females were 9 May; seven species from the same localities were reproductive in April. I have also obtained ripe females in late June supporting Hill's report of early July reproduction.

Niangua darter.—Pflieger (1975) reported spawning activities by *Etheostoma nianguae* in early April. My documentation of a ripe female on 20 April (Fig. 6) is in general agreement with Pflieger and suggests extended spawning.

Rainbow darter.—The reproductive season for *Etheostoma caeruleum* has been reported as late March to May in Missouri (Pflieger, 1975), early April to early June in Michigan (Winn, 1958) and April to June in Wisconsin (Becker, 1983). My Missouri data support the season reported by Pflieger (Fig. 6). My Arkansas data show spawning from late Feb. to late May. The reproductive season is two to three months in most areas.

Discussion

Darters in most geographic regions treated here have breeding seasons extending over several months. The cumulative data suggest that in stenothermal environments in Texas three darter species (*E. lepidum*, *E. grahami* and *E. fonticola*) are reproductive all year. In addition, fertilized eggs have been obtained over intervals of 273 (*E. lepidum*), 203 (*E. spectabile*), 150 (*P. sciera*), 143 (*P. caprodes*), 100 (*E. proeliare*), 99 (*P. shumardi*), 96 (*E. caeruleum*), 88 (*E. grahami*), 86 (*E. punctulatum*), 76 (*E. chlorosomum*) and 71 (*E. gracile*, *E. radiosum*, *E. tetrazonum*, *E. stigmaeum* and *E. flabellare*) days. Except for *E. blennioides* and *E. juliae*, the other species have data for fewer than five days of reproduction. If eggs have been removed from a female on only one occasion, obviously, only one reproductive day can be reported. Documentation of prolonged spawning must follow study over a protracted interval that is not available for the species with fewer than ten known days of reproduction. Thirteen species are known to be reproductive for more than two months. Each species has been shown to have most females in reproductive cycle throughout that interval; thus, individual females are reproductive for that time interval. Data on *E. lepidum* and *E. spectabile* suggest that interbrood intervals range from 4 to 10 days dependent upon stream temperature. Most streams are at 15–20 C during the reproductive season—at those temperatures interbrood intervals are 5–10 days. Therefore, females of the 13 species have the potential of a minimum of six spawnings annually; if the stream temperatures are warmer, the minimum number of spawnings would be 12. The maximum number of clutches per year is 73.

The spawning season for central Texas darters is long. The recorded season for *E. lepidum* is 273 days and ripe eggs have been obtained periodically during the other 93 days. The documented length of the season in individual stenothermal environments is 246 (S. Guadalupe), 215 (Mtn. Home) and 211 (S. Concho) days and that of extensively sampled eurythermal environments 164 (Junction), 167 (San Saba) and 162 (Ingram) days. Thermal stability plays a substantial role in the length of the reproductive season. Whenever the temperature becomes warm (=ca 24 C) spawning activity slows or ceases. Each eurythermal population shows spawning season initiation during declining daylength.

The breeding season for *E. spectabile* in Texas is quite similar to that of eurythermal populations of *E. lepidum.* The summed reproductive season is 203 days and individual populations are known to be reproductive for at least 147 (Ingram) to 187 (N. Guadalupe) days. The initiation of reproduction is consistently during periods of decreasing daylength. Marsh's (1980) documentation of extended spawning in artifically cooled waters shows that temperature has an effect on length of spawning season. No substantial shift in spawning season with latitude is apparent among Texas populations. There is a suggestion of a shift between the northernmost Texas sample (Lampassas) and the others as it starts last and ends last. The Arkansas populations have markedly shorter seasons (ca 100 days) than the Texas populations. The majority of the change is at spawning initiation (Feb. vs Nov.) with little change in last spawning (early June vs mid-May). The more northern populations continue the trend with shorter spawning seasons that start in March (Pflieger, 1975; Winn, 1958) and end in early June.

The breeding season for logperch in Texas is substantially shorter than that for either *E. lepidum* or *E. spectabile.* The cumulative season is 143 days and individual populations are known to spawn for up to 140 days. The major difference is in the date of first spawning (Dec. or Jan. vs Oct., Nov. or Dec.) and most Texas populations start spawning at the time of short daylength or shortly after. There is little difference in the date of reproductive termination in eurythermal populations. The breeding season for logperch in Arkansas (62 days) is shorter than that for Texas populations and again the majority of that difference is in reproductive initiation (Feb. vs March) not termination (mid-May vs early June). The spawning season in Missouri seems displaced seasonally but Pflieger's (1975) report of April breeding suggests that the actual season is April through early June, again different dates of spawning initiation and comparable termination dates. Winn's (1958) report of April to early June reproduction in southern Michigan is in accord with a delay in initiation of spawning but little difference in termination.

Geographic comparisons of spawning season within a species are in accord with a pattern of longer seasons in the south than in the north. Additionally, comparisons among geographically restricted species show the same pattern, with Texas species often spawning for most of the year, and those from Arkansas or Missouri spawning for two to three months. Few reports for more northern species are for more than two months of spawning.

The reproductive seasons for darters vary extensively from essentially continuous spawning in stenothermal waters in southern locations through prolonged winter/spring spawning in eurythermal waters in southern locations to relatively brief spawning at northern latitudes. Much effort has been focused on the causal factors for initiation of spawning but much less attention has been directed to causal factors for termination of spawning. Especially for organisms with substantial geographic variation in spawning seasons it is possible that different mechanisms could apply. The variations in the reproductive seasons for *E. spectabile* may provide insight into reproductive cues. Although annual clocks may play a role in reproductive stimulation, Marsh's (1980) demonstration of a change of the date of termination associated with an artificial change in environmental temperature suggests, at least, that termination is not totally dependent on an endogenous rhythm.

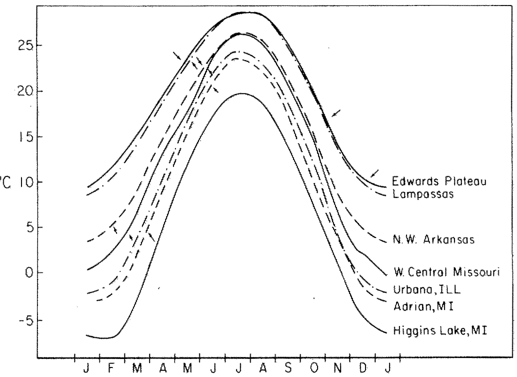

Fig. 7. Annual thermal cycles for seven locations derived from NOAA (1974). The localities are those closest to the regions most closely studied for darter reproduction in the central United States. Known dates for *Etheostoma spectabile* reproductive initiation and termination are designated by arrows.

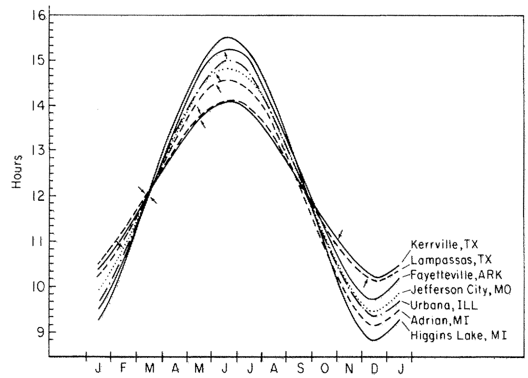

Fig. 8. Annual light cycles for seven localities derived from Smithsonian (1896). The localities are in the regions most closely studied for darter reproduction in the central United States. Known dates for *Etheostoma spectabile* reproductive initiation and termination are designated by arrows.

The commonly discussed environmental cues are light and temperature. In addition, food supplies must be sufficient to provide metabolites for gamete production; the wide scatter (standard deviation = 20 ± eggs) in fecundity of equal-sized females recorded for *E. lepidum* and *E. spectabile* (Hubbs et al., 1968) is best explained by variations in food supplies.

The air temperature cycles (Fig. 7) for the various locations inhabited by *E. spectabile* show the expected colder weather in more polar locations. In addition, the summer temperatures are more similar than are the winter temperatures. The major exception is that summers in northern Michigan (Higgins Lake) are about 3 C colder than in southern Michigan (Adrian) whereas the winters are only about 4 C colder. The same comparison between Lampassas, Texas, and NW Arkansas shows differences of 2 C and 5 C. The temperatures for first spawnings vary widely (17, 9.5, 5, 6, 5.5 C) from south to north. The distinction between southern and northern populations must be even greater than suggested by spawning dates as the stimulus for spawning must precede actual egg deposition. Thus, in the areas with the warmer temperatures an earlier date would have even warmer conditions and the areas with the colder temperatures would be even colder than these of the actual spawning date.

The pattern of environmental temperatures for spawning termination shows much more similarity with all between 21.5 and 23.7 C. Those data reflect the last known date for spawning and if a stimulus period is considered, the most northern population has the lowest spawning thermal maximum and the slowest warming. Thus, a time lag between the cue to stop spawning and the actual stop would have the greatest thermal consistency among the cue temperatures in northern populations. The major exception in termination of intraspecific spawning seasons is the later time for *P. caprodes* in northern Michigan; however, it is this area that has much reduced mid-summer warming.

The pattern of light cycles and spawning intervals shows the opposite pattern (Fig. 8). Spawning initiation is 9 hrs 10 min daylight to 12 hours daylight. In this instance the short daylength is for southern locations and any stimulus would involve a prior interval with longer daylight; the longer daylight figures are for northern populations and for these the preceding intervals are for less daylight. In effect, daylength for initiation of reproductive stimuli is likely to be reasonably concordant among the populations. The major difference would be that for southern populations it occurs in decreasing daylength and it would be likely to involve increasing daylength in northern populations.

There is somewhat less variation between daylength of last spawnings between 13 hrs 40 min daylight in the south and 15 hrs 10 min in the north. Although the variation of daylength at end of spawning is not dissimilar to those for spawning initiation, they also correspond well with season of the year. More critically, the substantial change in date of spawning termination with thermal change (Marsh, 1980) suggests a major role of temperature in determining the end of the spawning season. An hypothesis that temperature plays a major role in spawning termination is supported by the year-round spawning of populations (*E. lepidum*, *E. grahami*, *E. fonticola*) inhabiting stenothermal waters. Simply, some factor has turned on reproduction and a thermal turn-off would not occur as females would not experience that level of thermal extreme during their entire lives.

The experiments on *E. lepidum* by Hubbs and Strawn (1957a) should be reevaluated in this context. Reproductive females continued to deposit eggs throughout their lives at varied daylengths between 0 and 24 hours light. No difference in egg production could be correlated with daylength. However, when the water temperature was raised from 20 to 23 C, there was a marked drop in reproductive activity. This correlates well with the observed temperatures in the environment when reproduction ceases (in Texas eurythermal environments they are the same as for *E. spectabile*). Additionally, the temperature (24 C) above which *E. lepidum* egg incubation success is low (Hubbs, 1961; Hubbs et al., 1969), is quite similar to that at which reproduction ceases.

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