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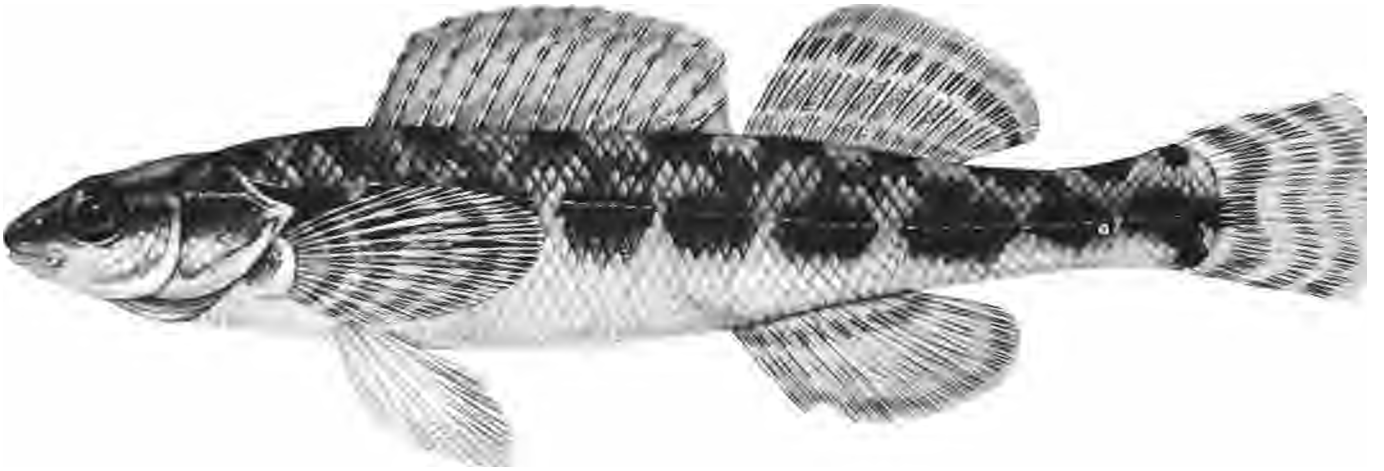

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THE LIFE HISTORY OF THE DUSKY DARTER, *PERCINA SCIERA,* IN THE EMBARRAS RIVER, ILLINOIS

Lawrence M. Page and Philip W. Smith

THERE ARE OVER 100 DESCRIBED SPECIES of darters, which represent marked degrees of adaptation and show considerable variation in ecological and reproductive characteristics. A few species have been studied in detail, and certain aspects of the life histories of several have been investigated (see Literature Cited sections in Winn 1958a and Braasch & Smith 1967), but for most of them ecological information is limited chiefly to observations on their habitats in different parts of their ranges. Among the latter are the species in the subgenus *Hadropterus* of *Percina,* for which habitat requirements have been recently described (Suttkus & Ramsey 1967) but for which reproductive habits, growth, diet, and demographic parameters remain virtually unknown.

The subgenus *Hadropterus* included only *nigrofasciatus* Agassiz, 1854, and *scierus* Swain, 1883, until the recent descriptions of *lenticula* Richards & Knapp, 1964, and *aurolineata* Suttkus & Ramsey, 1967. Three of the species are restricted to the Gulf and Atlantic coast drainages; the fourth *(sciera)* is more widely distributed and is the subject of the present study.

The dusky darter was described as *Hadropterus scierus* from Bean Blossom Creek, Monroe Co., Indiana (Swain 1884:252) and, except for brief assignments to the genera *Serraria* and *Etheostoma,* was so known until Bailey, Winn, & Smith (1954:140) reduced the number of darter genera to three and relegated *Hadropterus* to subgeneric rank. Currently, the species is regarded as consisting of two subspecies, the northern dusky darter *(Percina s. sciera)* and the Guadalupe River dusky darter *(P. s. apristis* Hubbs, 1954), an endemic in the Guadalupe River system of Texas.

Percina sciera (cover illustration) is a large darter, with the adults ranging from 2 to 4 and occasionally 5 inches in total length. The adult is light olive-green dorsally, with a pattern of black or brown markings, and nearly white below. A dark band extending around the snout, through the eye, and across the opercle connects to a broken lateral band of 7-12 large, dusky, oblong blotches on each side. The latter alternate with 7-10 dark blotches, which cross the midline of the back. Three vertical dark blotches on the caudal fin base form a distinctive, partially fused bar. A dark teardrop is usually lacking. The fins are nearly transparent but have small pigment spots along the spines and rays, which give the appearance of faint bars.

The male differs from the female in having a midventral row of large and strongly toothed scales and a smaller and less rounded genital pore.

The young of *P. sciera* are distinguishable from the young of the superficially similar *P. maculata* and other species of *Percina* in the Wabash drainage by the distinctive fused blotches on the base of the caudal fin.

The dusky darter occurs from the Elk River of West Virginia (Richards & Knapp 1964:700), Tennessee River system of Kentucky and Tennessee, and the Black Warrior-Tombigbee system in Alabama southward to the Gulf Coast (Suttkus & Ramsey 1967:138) and westward through Mississippi and Louisiana to central Texas, southeastern Oklahoma, and southeastern Missouri (Trautman 1957:535). Its range extends northward to eastern Illinois, throughout most of Indiana with the northernmost record in the upper Tippecanoe River (Gerking 1945:85), and into the Scioto River drainage of south-central Ohio (Trautman 1957: 535). In Illinois the species is restricted to the Ohio-Wabash drainage, and it is common only in the Embarras River and Middle Fork of the Vermilion River and their tributaries (Fig. 1).

We are indebted to Raymond T. Schaaf, Hartley F. Hutchins, Dorothy M. Smith, Norman D. Penny, and the late Robert L. Hass for aid with field work; to our associates Donald W. Webb, John D. Unzicker, Milton W. Sanderson, and Herbert H. Ross for helping with identifications of arthropod fragments in the darter stomachs; to Marvin C. Meyer, University of Maine, for identifying a leech parasite; to Harmon F. Smith, Illinois State Water Survey, for providing data on water chemistry of the Embarras River. We are grateful to Richard M. Sheets, Survey technical illustrator, for preparing the illustrations, except those of the darter which were done by Alice Ann Prickett, University of Illinois School of Life Sciences; to Wilmer D. Zehr, Survey photographer, for the photographs; to our colleagues W. C. Childers and J. A. Tranquilli for temporary use of one of their aquaria and R. W. Larimore for lending us a 30-foot electric seine and 115-v generator.

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COVER ILLUSTRATION: Adult female *Percina sciera sciera* collected in October in the Middle Fork, Vermilion County, Illinois. From a watercolor by Mrs. Alice Ann Prickett.

The manuscript was edited by 0. F. Glissendorf, technical editor at the Survey. Edward C. Raney, Cornell University, served as special guest reviewer.

THE STUDY AREA

The area selected for study was the middle Embarras River in the vicinity of Greenup, Cumberland Co., Illinois. Less disturbed than most other local streams, the Embarras supports an exceptionally large number (14) of darter species, of which *P. sciera* is the most abundant.

The Embarras River, a tributary of the Wabash, has its headwaters in Champaign County and meanders southward through rich farmland on Wisconsin glacial till until it cuts through the Shelbyville Moraine near Charleston in Coles County. For several miles downstream from Charleston the river has deposited large quantities of glacial gravel from the thick morainal deposits. Near Newton in Jasper County it veers

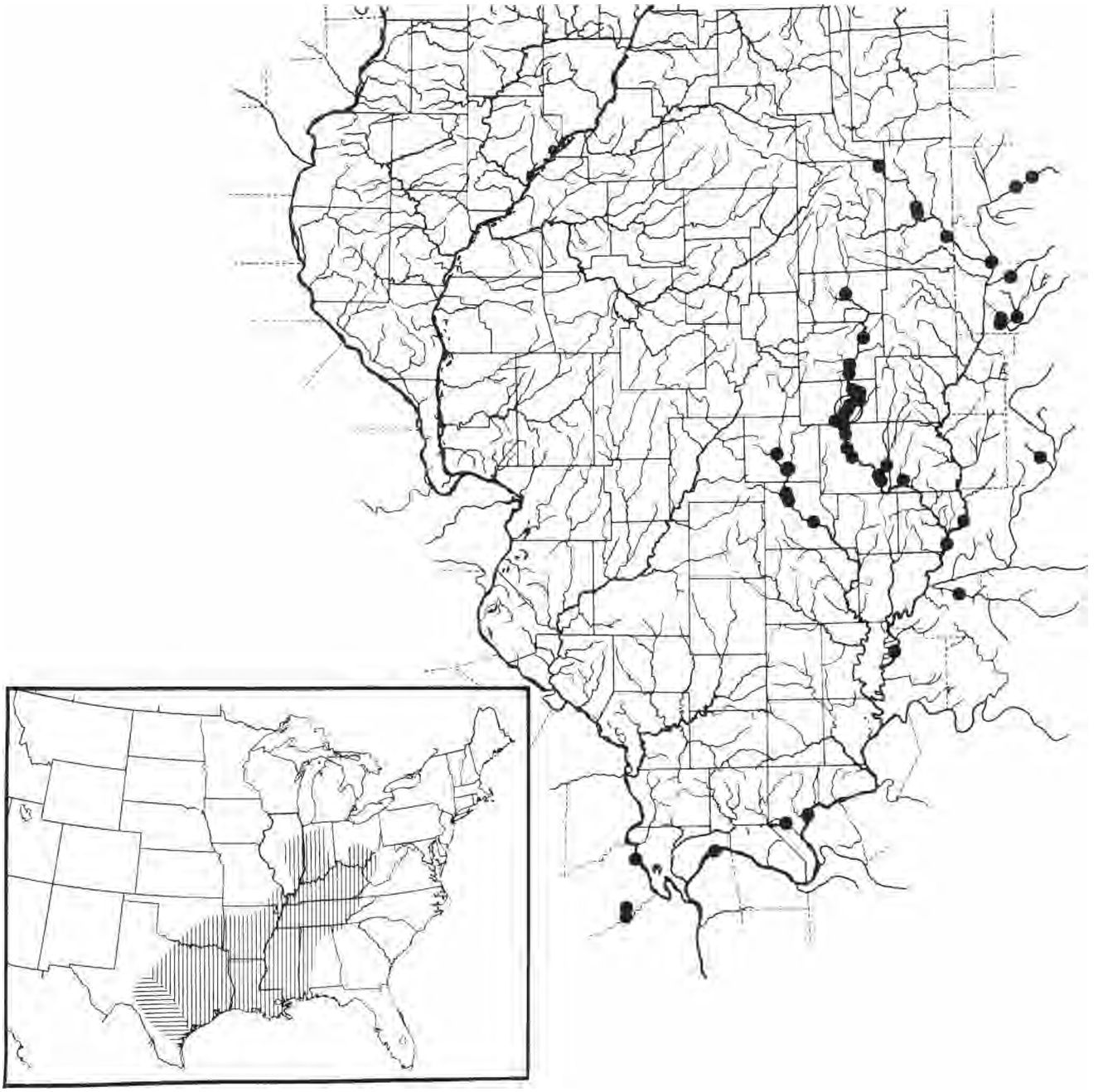

Fig. 1. —Distribution of *Percina sciera* in Illinois and adjacent Indiana and Missouri and the total range (inset) of the species. Some of the Indiana records are from Gerking (1945:85). On the Illinois map the study area is encircled (at heaviest cluster of dots); on the inset map vertical hatching represents the range of *P. s. sciera,* horizontal hatching that of *P. s. apristis.*

toward the southeast and flows over a bed of predominantly sand and Illinoian clays. The river empties into the Wabash River near Billett, Lawrence County, having drained about 2,400 square miles in its approximately 180-mile course through eastern Illinois.

Chemical measurements taken in the Embarras River at Camargo in Douglas County from October, 1966, to April, 1968, by the Illinois State Water Survey,

Fig. 2. — Two stations in the study area: Embarras River 1 mile west (top) and 3 miles southwest (bottom) of Greenup, Cumberland County, Illinois.

and made available through the courtesy of Harman F. Smith, indicated that the water quality was unusually high and pollution was minimal. Average chemical values were: total phosphates 1.2 ppm, nitrates 25 ppm, sulfates 69.7 ppm, and ammonium compounds 0.1 ppm. The alkalinity averaged 199 ppm, hardness 285 ppm, and total dissolved minerals 376 ppm. Turbidity varied during this period from 2 ppm to 138 ppm.

In the vicinity of the study area the stream could be classed as a small to medium-sized river. During low water stages the channel was only 15 to 30 feet wide and in riffle areas barely a foot in depth, although there were some deep pools at bridge sites and at abrupt bends in the river. During flood stages the floodplain was inundated, and the river was almost 1 mile wide.

The study area consisted of a 5-mile stretch of the river (the encircled area in Fig. 1) and several nearby locations, which were sampled when the main stations were inaccessible because of high water. One of the principal sites (Fig. 2, top), one mile west of Greenup, had a variety of habitats — gravel bars and gravelly raceways, sand bars and sandy raceways, a rubble riffle, and several silt-bottomed pools. Another site (Fig. 2, bottom), 3 miles southwest of Greenup, was similar but had more extensive stretches of sand bottom and lacked rubble and strong riffle areas.

METHODS

A total of 37 collecting trips was made to the study area between August 4, 1967, and July 1, 1969. Initially various habitats were sampled to determine habitat preferences; later efforts were concentrated in the channels, where the darters were usually abundant and more easily obtained. Collections were made by minnow seine at approximately 2-week intervals from August to November in 1967 and at irregular intervals throughout 1968 and early 1969 in an effort to obtain as much information as possible for all seasons. Considerable difficulty was encountered in obtaining specimens during several periods of high water, but eventually specimens were secured for every month except January. Specimens collected during the 2-year study period were distributed as follows: February, 12; March, 8; April, 6; May, 27; June, 26; July, 20; August, 48; September, 60; October, 53; November, 38; and December, 2, for a total of 300 specimens.

Supplemental collections from previous years in the same area provided additional specimens and helped fill gaps resulting from flood periods. A total of 526 preserved specimens were examined during the study for information on food and reproduction within the study area, but the information on growth and other facets of the life history were based on the 300 specimens secured during the study period.

Specimens from the study area were measured, their age and sex were determined, and details of color pattern and the presence of external parasites were noted. Young darters were examined for developmental features and for growth. Most of the adults were dissected and gonad conditions were noted. As spawning time approached, the dimensions of gonads were recorded and ovarian egg counts were made on several females. Age determinations were made by counting the number of annuli on scales removed from the dorsum on the left side of the body near the junction of the spinous and soft dorsal fins.

The stomachs of most of the adults and 20 percent of the young were examined for food organisms. Stomachs of some potential predators of P. sciera were also examined for darter remains.

During the spring, water and air temperatures were routinely taken, and notes were made on the river and weather conditions, coloration of the fish, and habitats in which specimens were captured. Care was taken not to deplete the darter population, and no more than 35 specimens were taken, even when the species was abundant and easily captured. Specimens were dropped into approximately 10-percent formalin as soon as they were captured.

Living specimens were brought to the laboratory from time to time so that their behavior could be observed in aquaria. When it became evident that captives were not going to spawn in the laboratory, eggs and sperm were stripped from ripe adults into petri dishes and kept until the eggs hatched.

On October 17, 1967, a quantitative sample was taken one-half mile north of Greenup with an electric seine to estimate the composition of the total fish fauna at the site, the numerical relationships of the component species, and the number of individuals per square yard of habitat. A 150-foot stretch of the river was blocked off by minnow seines held in place by steel rods, so that fishes could neither enter nor leave the enclosed area, and the number of square yards was calculated. A 30-foot electric seine with 15-inch drop cords at 30-inch intervals was moved from the downstream to the upstream block repeatedly in an attempt to kill all fishes in the enclosure. Dead fishes were picked up by hand and with dipnets in clear water; those in deep or turbid pools where they could not be seen were removed by repeated seining of these pools.

HABITAT AND ASSOCIATED SPECIES

In the study area all sizes of P. sciera were most often found in that portion of the river channel that had a combination of gravel bottom, rapid or fairly rapid current, and a depth of at least 1 foot. The species was seldom found over bottom materials other than gravel and never found in quiet pools or shallow water. Accumulations of branches and leaves in the gravel of the channel often contained darters, suggesting that these were hiding or resting sites. Captive darters hid under large rocks or other objects on the bottom of the aquarium.

In Ohio a preference on the part of dusky darters

for rooted plants was noted by Trautman (1957:536); however, no rooted plants were present in our study area, and the species was abundant. Elsewhere in its range, this darter is reportedly common in habitats free of aquatic vascular plants (Blair 1959:10; Gerking 1945:85; Suttkus & Ramsey 1967:140).

Lotic habitats in moderate-sized creeks to large rivers are occupied by *P. sciera.* In the study area streams only 6-8 feet wide contained the species at least in the summer months. Records are also available for such large streams as the Wabash, Ohio, and Mississippi rivers.

An opportunity to quantify the relative abundance of associated species was available with the use of the electric seine in the section of river blocked off with seines, and it provided a concept of the ecological community of which the dusky darter was a component. Within the enclosed 507 square yards of water averaging 1 foot in depth, 750 fishes of 18 species were collected. The minnows *Pimephales vigilax, Notropis whipplei,* and *Notropis spilopterus* were clearly the most abundant associated species (Fig. 3), their combined totals comprising 78 percent of the total number of fish present. Other frequent associates were the minnows *Phenacobius mirabilis, Ericymba buccata,* and *Cain postoma anomalum,* and the hog sucker *Hypentelium nigricans.*

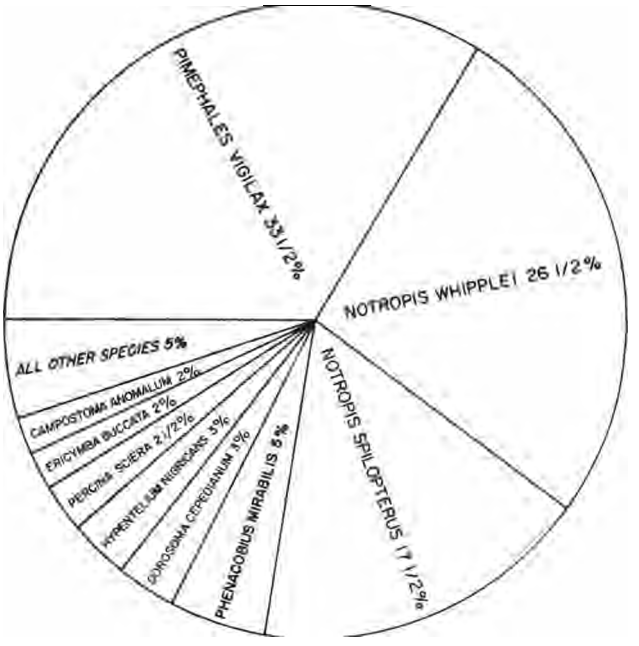

Fig. 3. — Relative abundance of fish species associated with *Percina sciera* as determined by a quantitative sample from the Embarras River near the study area.

Percina sciera ranked seventh in abundance (2.5 percent of the total number of fish) and was more than five times as abundant as the second most abundant darter, *Percina phoxocephala.* Other darters found in the study area were *Etheostoma blennioides, E. caeruleum, E. nigrum, Ammocrypta pellucida, Etheostoma spectabile, Percina maculata, P. caprodes, Etheostoma asprigene, E. chlorosomum, E. gracile, E. flabellare,* and *E. histrio.*

REPRODUCTION

Reproductive Cycle of the Male

Most males were sexually mature and ready to spawn the first spring following their hatching. Of seven males approximately 1 year old collected May 27, 1969, one 48 mm in standard length had undeveloped testes and no indication of breeding coloration, but six others more than 55 mm in standard length were more darkly pigmented and appeared ready to spawn at that time. However, yearling males were smaller and had less intense breeding colors than older males and were probably at a disadvantage in attracting females.

As the breeding season approached, an over-all duskiness masked the normal olive-green ground color, and the row of lateral blotches became obliterated by blackish vertical bands which were narrowly **but** distinctly separated from each other. The top of the head, belly, breast and fins also darkened, and a dark blotch developed on the posterior portion of the spinous dorsal fin. A faint, pale orange band appeared on the distal part of the spinous dorsal fin.

Each scale on the dorsal half of the body could be seen, with magnification, to be sprinkled with several brilliant blue-green iridocytes that gave the fish an iridescence. Melanophores concentrated on the subdistal portion of each pelvic fin and the soft dorsal fin to form a discrete, thin, pigmented band margined distally by a transparent band (Fig. 4).

In our study period, the earliest specimen that showed pronounced breeding coloration was a 2-year-old male collected on April 28. He was darkly pigmented over the entire body and had developed the dark vertical bands and dark blotch at the posterior base of the spinous dorsal fin. The height of breeding coloration was reached in late May, when large males lost the vertical bands and became almost uniformly black.

Breeding males did not develop tubercles, and according to Collette (1965:577) none of the species of the subgenus *Hadropterus* has breeding tubercles.

The development of the testes consisted of a gradual increase in size until spawning and then underwent a sharp decrease. In a September-collected male, the length of one testis was 10 percent of the standard length; in a March specimen, 13 percent; in May and June specimens, 14 percent; but in a July specimen, only 8 percent.

Reproductive Cycle of the Female

Like males, females usually were sexually mature at 1 year of age **but,** unlike males, they were ready to spawn at a smaller size (approximately 40 mm in standard length). Yearling females collected in May

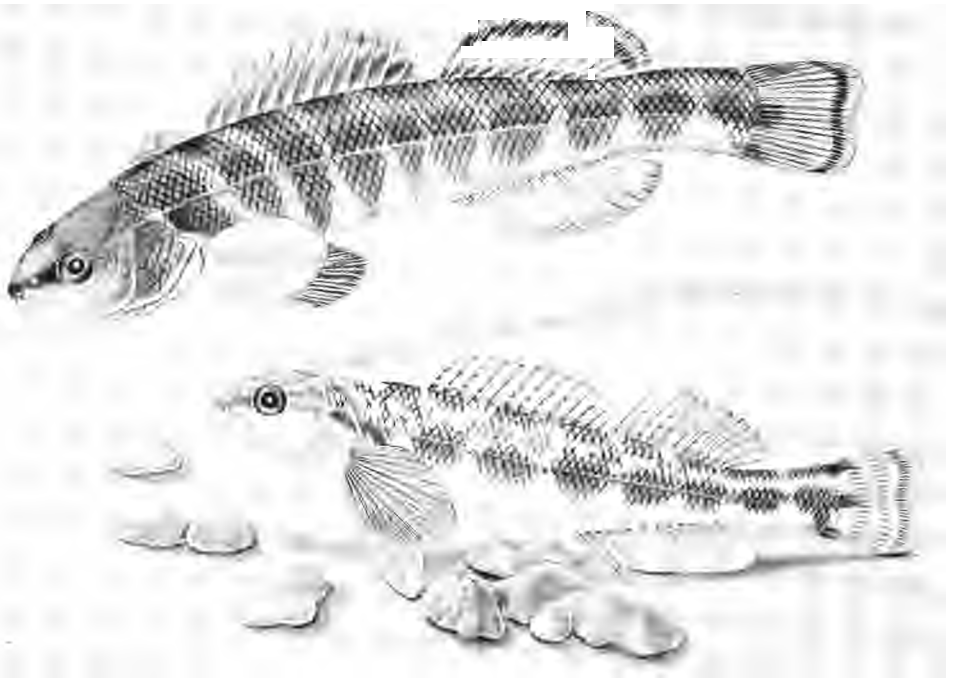

Fig. 4.—Pigmentation patterns of breeding male and female *Percina sciera.*

and June less than 40 mm lacked mature eggs, but larger yearlings collected at the same time and place contained mature eggs and appeared ready to spawn.

The reproductive cycle of the female was divisible into a prespawning period, the spawning act, and postspawning period. The prespawning period was characterized by the differentiation and maturation of ova, the spawning act by the release of mature eggs, and the postspawning period by absorption of the remaining ova and recovery of the ovaries.

Two characteristics of ova maturation — size and color — were easily observable and allowed the developing ova to be categorized. The ova were all small in the earliest stages of maturation, but in late spring when development was most rapid the ova were consistently present in three different size groups: less than .5 mm, between .6 and 1.0 mm, and from 1.1 to 1.5 mm in diameter. The smallest ova were white, the intermediate ones were yellow, and the largest were dark yellow or orange.

Percentages of differentiated ova (Table 1) were based on estimates rather than actual counts but the estimates were consistently made and are comparable. The prespawning period began when the ova first began to differentiate in early October. A specimen collected in September had almost no ova that could be classed as differentiated, but one collected on October 14 had an estimated 10 percent of the ova differentiated, although they were still white and less than .5 mm in diameter. The initiation and progression of ova development may vary with the size and age of the fish and possibly with climatic conditions.

Early stages of differentiation proceeded slowly, and not until the water warmed and spawning time approached did recognizably mature eggs appear (Fig. 5). Examination of a specimen collected on March 7 indicated that as many as 90 percent of the ova had differentiated but all were white and less than .5 mm, just as those of the October specimen had been.

A specimen collected on April 28 contained ova clearly divisible into the three size and color categories mentioned above (the smallest ova were white and less than .5 mm in diameter, the intermediate ova yellow and between .6 and 1.0 mm, and the largest orange and between 1.1 and 1.5 mm). Sixty-four per-

TABLE 1.—Differentiation and growth of ova in *Percina sciera* collected in the study area between August 4, 1967, and June 8, 1969.

Date of Collection	Estimated Percent of Differentiated Ova	Percent of Differentiated Ova by Size Group		
		.1—.5 mm	.6-1.0 mm	1.1-1.5 mm
Oct. 14	10	100		
Nov. 1	15	100	0	
Dec. 7	25	100	0	
Feb. 23	80	92	8	0
Mar. 29	75	69	31	0
April 28	over 90	64	25	11
May 15	over 90	64	24	12
June 25[a]	over 90	60	26	14
July 7a	over 90	56	24	20
Aug. 4	10	100		
Sept. 21	0			

[a] 1968 only; in 1969 *Percina sciera* spawned in early June.

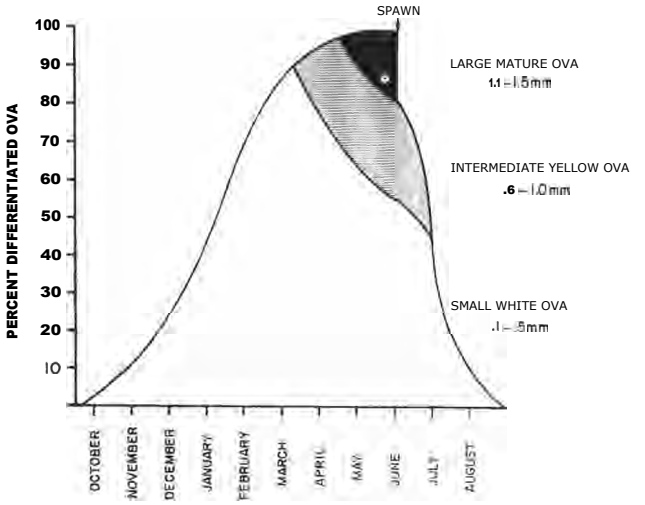

Fig. 5.—Differentiation of ova during the year, as inferred from data in Table 1.

cent were in the small-ova category, 25 percent intermediate, and 11 percent in the large-ova group.

The general pattern of differentiation during the spring months was a decrease in the percentage of small ova and an increase in the percentage of large ova (Table 1). The number of intermediate ova after April remained approximately the same (Fig. 5). Essentially the same pattern was found in *Etheostoma gracile* by Braasch & Smith (1967:6), but they also found a general increase in the relative proportion of intermediate ova present.

The ovaries of the dusky darter gradually increased in size during the prespawning period (17 percent of the standard length of a September specimen, 21 percent in a March specimen, 27 percent in an April specimen, 35 percent in a May specimen, and 34 percent in a June specimen) as the eggs developed. The gradual enlargement of the ovaries coincided with enlargement of the testes in the male; both showed most pronounced increases in April and reached their greatest sizes in May and June. The ovaries of postspawning females were greatly reduced in size.

Between 500 and 2,000 ova were produced by one female in one season, but only about 10 percent reached mature size. The number of mature eggs in specimens examined ranged from 80 to 196. Although an actual count of eggs laid by a dusky darter could not be made, other studies on darters indicate that they normally lay the total complement of mature eggs (Fahy 1954:166; Winn 1958a:181). A relationship exists between the size of the female and the number of eggs produced, the larger females producing more eggs.

Mature ova tended to be concentrated near the center of the ovary and, in preserved specimens, were easily detached from the surrounding tissue.

Following the act of spawning, unlaid eggs atrophied and were ultimately absorbed. The ovaries gradually shrank and lost the yellow-orange color. A quiescent or recovery stage followed the absorption of the egg materials, during which time no egg development was detectable.

As spawning time approached, the genital papilla enlarged, becoming tubular, and the breeding colors intensified. The breeding female became more intensely colored; the yellow color of the dorsum became brighter, the undersides remained white, and the lateral blotches appeared more intense. While the melanophores of the breeding male were jet black and interspersed with numerous blue-green iridocytes, melanophores of the breeding female were brown in color and iridocytes were sparse. The striking yellow of the dorsum resulted from concentrations of yellow pigment along the posterior edge of each scale.

Spawning

The dates of spawning and duration of the spawning period appeared to vary from year to year, probably as a result of climatic and river conditions. In 1967, juveniles collected on August 4 averaged 30 mm in standard length, and to have attained such a size the eggs were probably laid sometime in July.

In 1968, darters could not be obtained in June because of high water, but on July 7 six adult females were captured. One appeared to be in an immediate postspawning condition and five contained large numbers of mature ova, indicating that they had not yet spawned. It is probable that the peak of the 1968 spawning was in early July. However, a 26-mm young collected on July 7 was the result of a spawning perhaps as much as a month earlier.

In 1969, peak spawning occurred between May 27 and June 8. Females collected on the first date were filled with mature ova; most of those collected on June 8 had spawned and were without mature ova. On both dates both males and females were very abundant in the shallower portions (1-3 feet deep) of the gravel raceway, the apparent spawning habitat.

The Embarras River was subject to several floods during the study period, and the unusually deep channels, inundated floodplains, and turbid water could have hindered spawning. The comparatively late spawning in 1968 (and perhaps also in 1967) is assumed to have been late because of the June floods. It appears that spawning in June is the preferred time for the species at this latitude.

Reproductive behavior is varied in darters, and the relative complexity is believed to be correlated with the extent of specialization. Little information is available on the mating behavior of *Percina,* the principal published studies being those for *P. peltata* (New 1966; Loos & Woolcott 1969), *P. notogramma* (Loos & Woolcott 1969), *P. caprodes* (Winn 1958a, 1958b: 192-194), *P. inaculata* (Petravicz 1938; Winn 1958a, 1958b:194), and *P. copelandi* (Winn 1953, 1958a, 1958b:202).

Although actual spawning was not observed, some

inferences can be drawn from observations on aquarium-held fish and from the morphology of *P. sciera* and its relationships to species in which the spawning behavior is known. Aquarium-held males during late May and early June underwent an array of color changes in response to particular stimuli, including the proximity of females. The only sexual behavior on the part of males, other than metachrosis, was an observation of tail-beating by a male sitting directly in front of a large female. A pair of newly captured darters was placed in an aquarium on May 28, 1969, and within a few hours the female appeared ready to spawn, repeatedly swimming over the male and alighting in front of him The male did not respond, and 24 hours later the female had apparently lost interest.

The presence of increased sexual dimorphism (larger size and darker color of male) in the spring suggests that sex recognition in the species is good. The generalized condition of a midventral row of specialized scales suggests that the male mounts the female and aligns his body with hers during fertilization and deposition of the eggs in a manner similar to that of *P. peltata* and *P. notogramma*. It is likely that spawning in *P. sciera* is no more elaborate than a free scattering of eggs over the gravel substrate, fertilization, and with that, the spawning act is completed.

DEVELOPMENT AND GROWTH

Development

Observations of the development of egg, embryo, and larval forms of *P. sciera* were made from June 8, 1969, when eggs and sperm were successfully stripped from a pair of adult fishes, to June 19, when the fry died.

The eggs were transparent, spherical, and adhesive. They averaged 1.5 mm in diameter and had a yellowish oil droplet .6 mm in diameter. At 36 hours the typical embryo, developing at 74-78°F, was 3.0 mm long. Midbrain and forebrain regions, optic vesicles, otic vesicles, and somites in the trunk region were clearly defined. The heart was beating and body contractions were frequent. No melanophores were visible.

At 60 hours, the dusky darter embryo was 4.8 mm long. The eye was heavily pigmented (black). A fin fold extended from the yolk sac ventrally to approximately one-half of the length of the embryo dorsally. The number of somites ranged from 26 to 29. Melanophores were scattered over the lower portion of the yolk sac. Unpigmented cells were visibly moving through the vitelline veins and dorsal aorta. The embryo was quite active and had a heart rate of 140 beats per minute.

At 65 hours, the blood was noticeably pink, and melanophores were present along the ventral side of the tail. At 84 hours, the eyes were metallic brown in color, and fin buds had formed.

At 74–78°F the darters began hatching at 90 hours and had all hatched by 108 hours. Hatchlings (Fig. 6) averaged 5.5 mm in total length. They had red blood, numerous melanophores on the ventral half of the body, and metallic gold eyes. In 2-day-old larvae the lower jaw was evident, rays had formed in the pectoral fins, and the yolk sac was small. At 3 days obvious breathing actions could be observed and at four days the fry were feeding on prepared food. At 5 days the yolk sac was gone and numerous melanophores were distributed along the myomeres. The fry died on the 6th day.

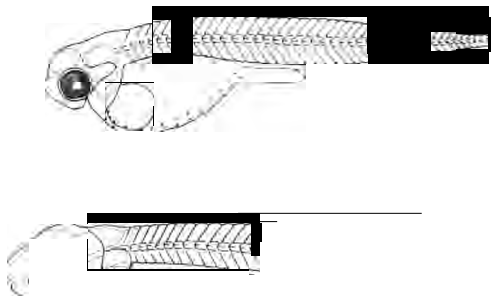

Fig. 6. — Development of morphological features of *Percina sciera* as illustrated by a hatchling and a 2-day-old larva.

The smallest specimen taken from the study area, a 15-mm (standard length) male (Fig. 7) collected on August 4, 1967, and estimated to be about 3 weeks old, had body proportions essentially those of adult fish but with characteristics reminiscent of the larval form. The head and eyes were large, and the fins were small in proportion to those of the adult. Squamation was incomplete but well advanced, the scales having formed over the body except for the area to either side of the anterior dorsal fin, the nape, and the anterior portion of the belly. Pigmentation was poorly developed, but the lateral blotches, the band around the snout, and spots of color in the fins were beginning to form. A short segment of the lateral line had formed in the region above the operculum but was absent on

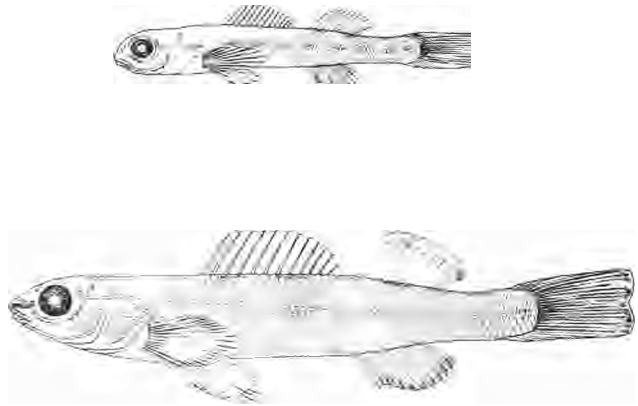

Fig. 7. — Juveniles 3 weeks (16 mm) and 5 weeks (26 mm) of age.

the rest of the body. The sensory canals on the head were present but incompletely pored, and the supratemporal canal was widely interrupted medially. The opercular spine was small and weak. The midventral specialized scales were not present.

In a 26-mm male (Fig. 7) collected at the same time and place as the 16-mm fish, the body proportions were more nearly those of the adult, except that the eyes were still relatively large and the fins proportionally small. Squamation was complete except on the nape. The pattern of pigmentation was that of adult fish, although less intense. The lateral line was complete. The head canals were complete and apparently fully pored, and the specialized scales were present on the midventer. In individuals 31- to 35-mm long, scales were present on the nape.

The basic color pattern of the adult was formed quite early, but pigmentation remained subdued throughout the first year. It intensified continuously thereafter, older fishes always being darker than younger ones in any given sample.

Growth

Standard length frequencies of specimens taken from the study area from August 4, 1967, to July 1, 1969, indicated rather rapid growth in the species, notably during the first few months of life. Presumably growth continues throughout life, but the rate diminishes with age.

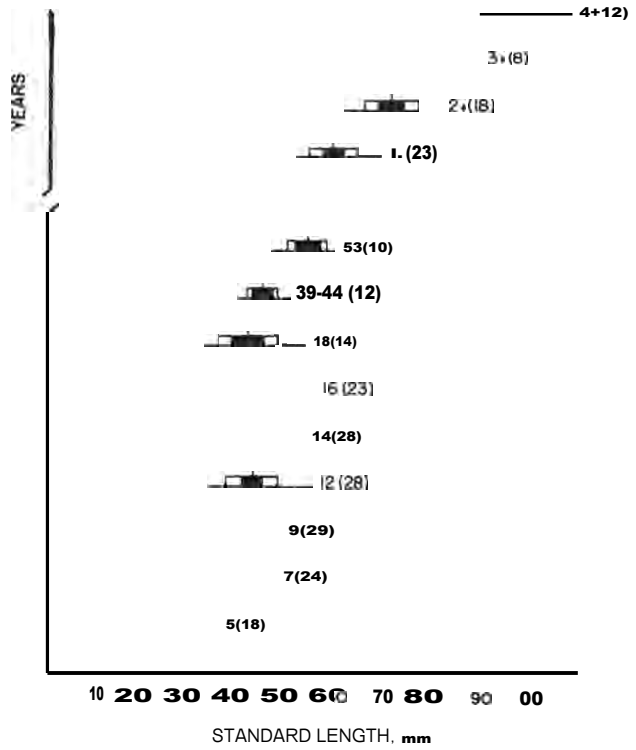

Fig. 8.—Growth of *Percina sciera* in millimeters standard length. The vertical line represents mean; horizontal line, range; hollow rectangle, one standard deviation to either side of mean; solid rectangle, two standard errors to either side of mean. Numbers in parentheses are specimens measured. Young in the first sample were estimated to be 5 weeks old; other samples were aged from the collection date of the first sample.

The growth data for samples taken from August, 1967, to July, 1968, (Fig. 8) showed a continuous average increase in size, except during late October (16 weeks) and November (18 weeks), when the mean standard lengths of two collections averaged less than those of the early October (14 weeks) collections. This reversal, which also occurred in samples from November, 1968, is assumed to be the result of an emigration of the larger fish from the comparatively shallow raceway being sampled to the deeper channel as winter approached.

In all but one sample of young taken in the study area, males averaged larger than females. The average standard length of darters between 1 and 2 years old was 57.5 mm for females and 61.4 mm for males; of those between 2 and 3 years old it was 62.3 mm for females and 73.3 mm for males. The largest specimen examined was a 4½-year-old male 108 mm in standard length collected November 1, 1968, in the Little Wabash River.

A transition from a predominantly pelagic to benthic swimming behavior was noted between young and adult dusky darters in aquaria. Young fish were active and spent most of their time swimming about and rarely resting on the bottom. Older fish, however, were usually quiet, occasionally darting about over the bottom or actively swimming.

PHYLOGENETIC RELATIONSHIPS

Within the subgenus *Hadropterus, P. sciera* and *aurolineata* are most alike in morphological features and least often found together where the ranges of all four members of the subgenus overlap. *P. nigrofasciata* appears to be more closely related to *P. sciera* and *P. aurolineata* than to *P. lenticula* (Suttkus & Ramsey 1967: 138) .

Among subgenera of *Percina, Hadropterus* appears to be intermediate between the more primitive *(Hypohomus, Swainia, Percina)* and the more advanced *(Cottogaster, Ericosma, Imostoma, Alvordius)* forms but probably is more closely related to the primitive subgenera. Primitive characteristics exhibited by *Hadropterus* include highly pelagic habits, large size, high meristic counts, and the modest specialization of the midventer row of scales in the males.

One of the anatomical features considered to be an indicator of phylogenetic position of darters is the degree of abatement of the gas bladder (Winn 1958a: 188). In *Etheostoma,* bottom-dwelling habits are accompanied by a reduction or loss of the bladder. In some species of *Percina* the gas bladder is present but small and in various stages of reduction. However, it is relatively large in *P. sciera,* indicating little phyletic

advancement. In three specimens examined, the gas bladder averaged about 16 percent of the standard length of the fish. In a 2-year-old male, 69 mm in standard length, it was 10 mm long, 3 mm wide, and 2 mm deep.

POPULATION CHARACTERISTICS

Density

Some information on population density of P. sciera in the middle Embarras River was provided by the electric-seine sample described earlier. The approximately 507 square yards of river (average depth 1 foot) yielded 750 fishes of various kinds for an average of 1.48 fish per square yard and one dusky darter for 25.3 square yards. However, rather than being uniformly distributed in the 507 square yards, the darters tended to occupy their optimal habitat, a gravelly raceway that comprised about one-fourth (127 square yards) of the area sampled. Thus a more realistic figure would be one dusky darter per 6.3 square yards of habitat.

Composition

Of the 20 dusky darters secured by shocking in the barricaded area, 17 (85 percent) were young-of-the-year and 3 (15 percent) were 1-year-old fish. The proportion of young to older individuals is remarkably similar to the age analysis made for all specimens examined during the 1967-1969 study period: 82.8 percent young-of-the-year, 13.7 percent yearlings, 2.7 percent second-year fish, and .7 percent third-year fish.

Approximately equal numbers of males (117) and females (124) were produced (Table 2), and the overall sex ratio of young can be assumed to be 1:1; however, males appeared to have somewhat greater longevity than females. Of 35 fish examined that were 2 or more years in age (including several not from the study area), 28 (80 percent) were males and 7 (20 percent) were females. However, females live to an age of at least 3 years, a fact substantiated by the presence in the Illinois Natural History Survey collection of a large female slightly more than 3 years old from Scott Co., Missouri. The oldest specimen examined was the previously mentioned 108-mm (standard length) male from the Little Wabash River of Illinois (4½ years).

TABLE 2.—Distribution of sexes and year classes in samples of Percina sciera taken from the study area between August 4, 1967, and June 8, 1969.

	Number by Year Class				
Sex	—1	1+	2+	3+	Total
Males	117	8	5	2	132
Females	124	32	3	0	159
Total	241	40	8	2	291

Although no evidence of predation on P. sciera was found, the primary control of population levels must be a combination of predation, the inherent limited longevity of the species, and the harshness of the physical habitat, particularly the fluctuations in the level of the river.

Migration

Although the dusky darter was the most common darter in the study area and consistently easy to collect during summer and fall, at times specimens could not be obtained. Sometimes they could not be collected because excessively high water prevented effective seining, but at other times (November of 1967, December of 1968) they could not be obtained even though the water levels were low and habitats in which the dusky darter had previously been plentiful were seined repeatedly.

Between October 3, 1967, when the species was very abundant (31 captured in 20 minutes) to November 4, 1967, when only 3 darters could be captured in 2 hours of seining, the population in the river channels had become greatly reduced. October 3 was clear, warm, and typically autumnal. By November 4. cold weather had begun and the air temperature was only 33°F. During this interval an emigration from the river channels to another habitat had occurred. By March, individuals of all sizes were again present in the channels.

Several species of darters are known to immigrate into tributaries in the spring, either to spawn and then immediately return to the habitat previously occupied or to remain throughout the summer and return to the river in the autumn (Lake 1936:817; Winn 1958a :163—164). Three tributaries of the Embarras River are located within 4 miles of the study area, and 18 collections have been made in them over the last 10 years. Three of 11 made in the summer months contained specimens of P. sciera, but none of the 7 collections made at other seasons contained specimens even when extensive effort was made and all types of habitats vigorously sampled in over a mile of the tributary, as was done November 25, 1967. Specimens had been collected in the same area in June of 1967, and several were collected the following day (November 26, 1967) in the Embarras River proper.

A winter movement out of the river channels and spring immigrations into them, followed by fall emigrations from tributaries, were the only migratory aspects observed in this study.

Territoriality

The presence of pronounced sexual dimorphism (larger size and darker color of the male) suggests that the male establishes and defends a territory. Aquaria used to hold dusky darters were evidently too small to allow the establishment of territories, and defended

areas were not well defined. However, certain males did select stations at which they remained, except to feed, and they were perpetually antagonistic toward any other males that approached their stations. No aggressiveness by males toward females or between females was noted.

DIET AND FEEDING HABITS

In 108 specimens of *P. sciera* examined for stomach contents, only current-dwelling insect immatures were found. The number of individual food items was often quite high, with as many as 116 and an average of 12.5 items per fish, but the variety of organisms was consistently low. During the entire study only midge larvae and pupae; larvae of caddisflies, black flies, and snipe flies; and naiads of mayflies and stoneflies were encountered in the stomach contents (Table 3). The principal food items were midge and black fly larvae, although some seasonal variation in the diet occurred (Fig. 9). Caddisfly larvae formed a large portion of the diet during the summer, and the dipterans and mayflies were the main components during other seasons. The variation was probably correlated with the relative availability of the different insect larvae throughout the year.

TABLE 3.-Stomach contents of *Percina sciera* of all ages collected from the Embarras River between August 4,1967 and June 8,1969. Figures in parentheses are numbers of stomachs examined.

Percent Occurrence of Food Organisms in Stomachs Examined

Food Organism	Feb. (10)	Mar. (8)	Apr. (6)	May (10)	June (10)	July (6)	Aug. (13)	Sept. (16)	Oct. (16)	Nov. (11)	Dec. (2)
Midge larvae, pupae	10.0	100.0	83.3	20.0	40.0	50.0			87.5	27.3	
Black fly larvae	70.0	37.5	83.3	80.0	50.0	33.3	61.5*	87.5	12.5	9.1	
Caddisfly larvae	10.0	....	....	10.0	20.0	83.3	15.4	25.0	37.5	9.1	
Mayfly naiads	10.0	....	33.3	40.0	70.0	66.7	15.4	75.0	50.0	18.2	
Snipe fly larvae	....		....	....	....	16.7	....	....	6.3	....	
Stonefly naiads		1.5									

Mean Number of Food Organisms Per Stomach

	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Midge larvae, pupae	0.4	8.9	2.5	1.0	1.4	2.2			7.9	1.5	
Black fly larvae	1.4	1.4	10.3	29.6	4.0	0.3	11.8*	10.3*	1.3	0.2	
Caddisfly larvae	0.1			0.1	0.3	16.2	0.2	2.2	1.4	0.2	
Mayfly naiads	0.1		0.3	1.9	2.5	1.8	0.8	4.9	1.3	0.2	
Snipe fly larvae						0.2			0.1		
Stonefly naiads		0.1									

Midge and Black fly larvae not separated in August and September.

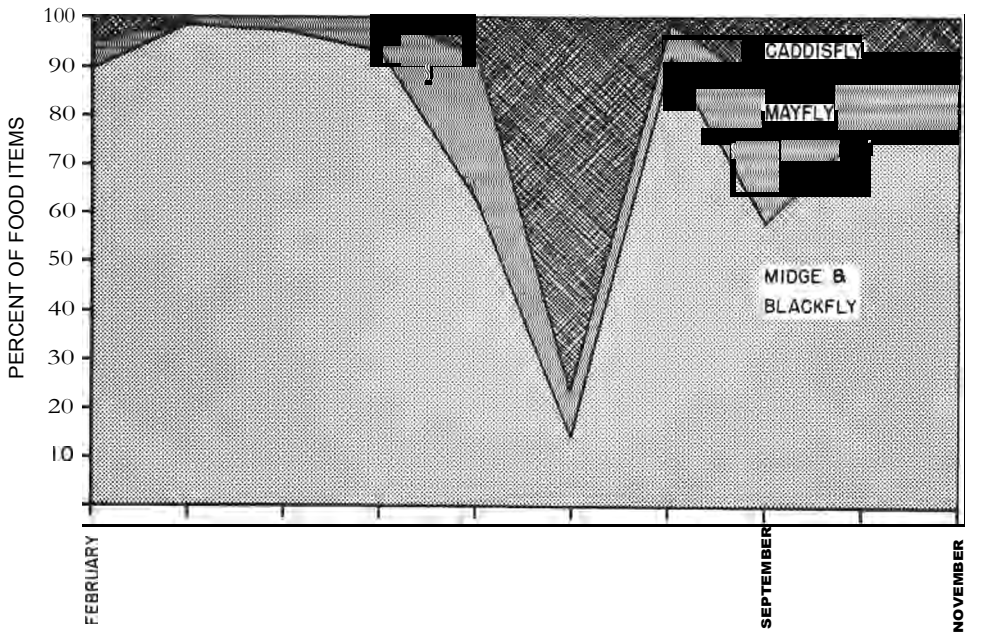

Fig. 9. - Seasonal variation in the diet of **Percina sciera** of all sizes. Percent of food item refers to total contribution in all fish examined each month.

Heaviest feeding occurred during May, just before the spawning period. Although feeding was reduced in winter as Fahy (1954:152) found in adult *Etheostoma blennioides*, some food ingestion probably occurs throughout the year. The deposits of fat around the intestine were approximately the same all year, except for the prespawning period during which time the gonads were developing and the amount of stored adipose tissue diminished. After spawning, the fat reserve was gradually replenished.

As the darters increased in size, there was a change in the over-all diet composition (Fig. 10). In fish less than 65 mm standard length, midge larvae were the predominant food item; caddisflies were seldom eaten. However, in fish 65-80 mm, the diet consisted primarily of caddisfly larvae. The average length of all darters containing caddisfly larvae was 63.5 mm, and for those containing dipteran larvae it was 50.1 mm. The proportion of mayflies and other miscellaneous food items was about the same in both small and large darters.

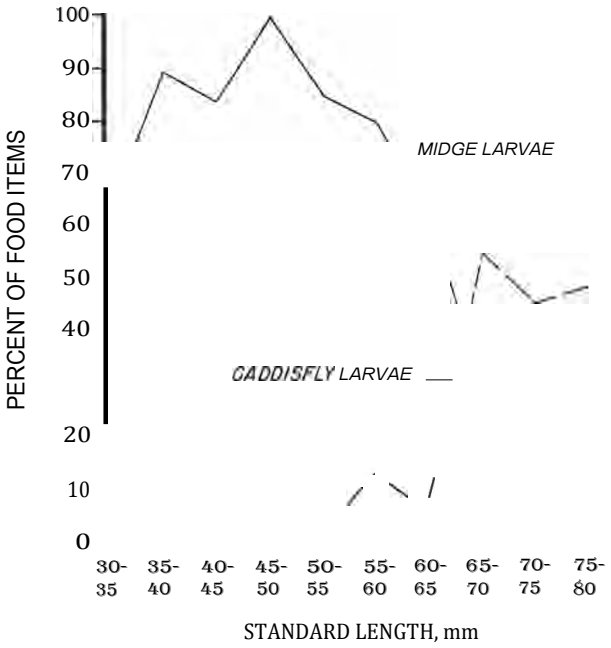

Fig. 10. — Change in relative consumption of midge larvae and caddisfly larvae as Percina *sciera* increases in size.

No data are available for the food of recently hatched young. In this study the smallest young contained dipteran larvae like those found in larger fish. However, the newly hatched darter, because of its small size, must feed for a time on plankton and other microorganisms, as the hatchlings of other darters are known to do (Braasch & Smith 1967:11). The main criteria determining differences between the diets of young and adult fish (Fig. 11) appear to be the size and availability of the prey item.

Aquarium-held specimens of P. sciera readily fed on mosquito wrigglers, phantom midge larvae, and sections of small earthworms.

INTERACTIONS WITH OTHER ORGANISMS

Competition

Limited information is available on the feeding habits of several of the fish species living in the study area. However, only those maintaining sizeable populations in the same habitat as the dusky darter needed to be considered as important competitors for food. The most likely of these was the slenderhead darter, Percina phoxocephala, which was rather abundant in much the same habitat and had a diet somewhat similar to that of the dusky darter. Slenderhead darters were noted to

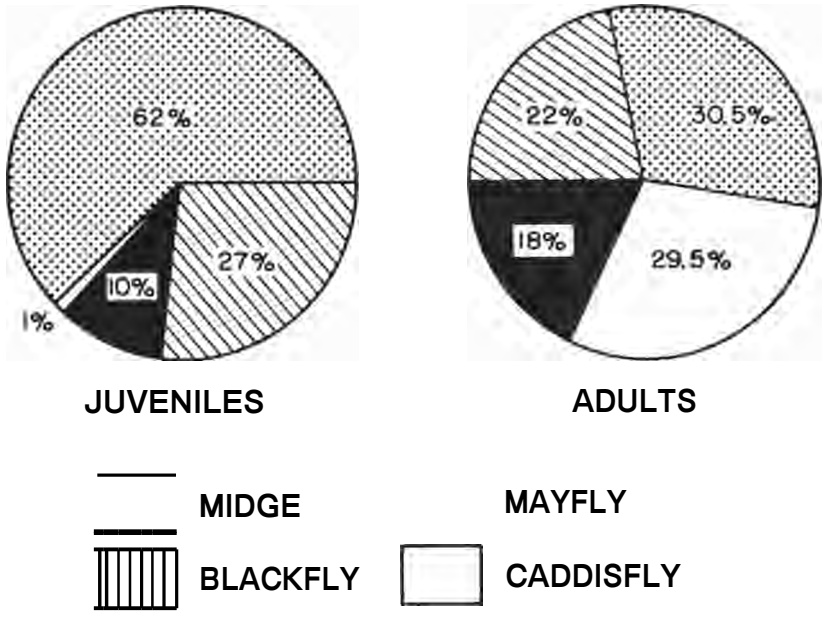

Fig. 11.—Composition of the diets of juvenile and adult Percina sciera collected in the study area from August 4, 1967, to July 7, 1968.

feed on mayfly larvae and pupae, dragonfly larvae, *Chironomus* larvae, and water bugs *(Corixa* sp.) (Forbes & Richardson 1920:286). Our examination of stomachs of *P. phoxocephala* in the Embarras River revealed a diet similar to that of *P. sciera,* but it included a greater variety of items. Some competition between the two species was suggested, but whether or not the food supply ever became low enough to cause population-limiting competition (demand in excess of supply) could not be ascertained. Collections of *P. sciera* examined throughout the year contained at least some specimens with full stomachs and thus competition for food was probably not a limiting factor for populations of *P. sciera.*

Competition for habitat space between *P. sciera* and most other darters occurring in the study area was also probably minimal because of differences in preferred microhabitat. For example, *Etheostoma blennioides* and *E. caeruleum* selected shallower, faster, and more rocky riffles. *E. nigrum* and *Percina maculata* preferred pools or slow-flowing raceways with sandy or silty bottoms. *Etheostoma spectabile,* which prefers headwaters and small tributaries, was uncommon in the river. *Ammocrypta pellucida* was rigidly restricted to sand-bottom areas. *Percina caprodes* and *Etheostoma histrio,* somewhat similar to one another in their habitat requirements in the Embarras River, selected fairly deep, rapid-flowing water with brush or debris on the bottom. Other species of darters were present in the study area only in extremely small populations.

However, *P. sciera* and *P. phoxocephala* appeared to be somewhat competitive for habitat and possibly breeding space inasmuch as they were the two most abundant darters in the study area and frequently were found together. *P. phoxocephala* is more plastic in its microhabitat choices, sometimes occupying swift water over sand, silty-sand bottom, or shallow riffles.

Competition for breeding sites was not likely among darters in the study area, inasmuch as, so far as breeding habits are known, all species except *P. phoxocephala* bred earlier than *P. sciera.*

Predation

No evidence of predation on dusky darters was found. By far the most abundant, large predaceous fish in the study area was the spotted bass, *Micropterus punctulatus.* Concurrent with the life-history study of the dusky darter, an investigation of the feeding habits of the spotted bass was conducted. The stomachs and intestines of 114 bass of various sizes were examined, and the only predation on darters noted was the remains of three specimens of *Etheostoma nigrum* (Smith & Page 1969).

Parasitism

A high incidence of leech parasitism was noted on dusky darters from June to November in the study area. A total of 109 leeches was removed from 249 darters examined for ectoparasites, most often from the proximal portion of the caudal fin. The leeches, identified as *Piscicolaria reducta* Meyer by Dr. M. C. Meyer, were more numerous on large darters, some having as many as four leeches. The number of leech parasites per fish on young darters examined was .39 (215 fish), on yearlings .57 (31 fish), and 2-year-olds 2 (3 fish). No other external parasites were noted.

Hybridization

Hybridization involving the dusky darter has been recorded in nature and as a result of experimental laboratory crosses. Hybrids between the dusky darter and blackbanded darter *(Percina nigrofasciata)* were reported by Suttkus & Ramsey (1967:141) from the Pearl River in Louisiana, and between the dusky darter and logperch *(Percina caprodes)* by Hubbs & Laritz (1961a) from the San Gabriel River in Texas. Also, an intergeneric hybrid between the dusky darter and orangethroat darter *(Etheostoma spectabile)* was reported by Hubbs & Laritz (1961b) from the San Marcos River in Texas.

Clark Hubbs and his students at the University of Texas have made artificial intergeneric and interspecific crosses involving the dusky darter and several other species of *Percina* and *Etheostoma* (Hubbs 1959; Hubbs & Strawn 1957).

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