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LIFE HISTORY OF THE FRECKLED MADTOM,
NOTURUS NOCTURNUS, IN MILL CREEK,
ILLINOIS (PISCES: ICTALURIDAE)

By

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The freckled madtom, *Noturus nocturnus*, is widely distributed in the lower and central Mississippi River basin and other Gulf of Mexico tributaries in Alabama, Mississippi, Louisiana and Texas (Taylor 1969; Map 4). The species is seldom found in large numbers and in spite of its wide range almost nothing is known concerning its life history. Taylor (1969), in his systematic revision of *Noturus*, described the external morphology, habitat occurrence and associated madtom species of *N. nocturnus*. Pflieger (1975) collected female *N. nocturnus* with fully developed eggs from southeastern Missouri in late May, and Cross and Collins (1975) stated that the species eats insects and small crustaceans in Kansas.

Larimore (1981) recently emphasized the need to accumulate information on all life-history aspects of warmwater fishes and the importance of even fragmentary observations. During a life history study of the brindled madtom, *Noturus miurus* (Burr and Mayden 1982), we collected some life history information on the syntopic *N. nocturnus*. Our purpose is to describe growth, reproduction, development, diet and demography of *N. nocturnus* in Mill Creek, Pulaski County, Illinois.

STUDY AREA

The study site, Mill Creek, a small tributary of the Cache River system (Ohio Drainage), 2.4 km NW of Ullin, Pulaski County,

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Illinois, was described by Burr and Mayden (1982). The study area is surrounded by cultivated fields and is a common dumping ground for trash by local residents; the large accumulations of cans, bottles and other debris probably contribute to suitability for reclusive madtoms.

Mill Creek has a few rocky or brushy riffles, pools with mixed mud, silt and rock bottoms, and in the study area has a width varying from 2 to 4 m and a depth varying from 0.5 to 1.5 m. Stream banks are steep and brushy and were tree-lined until recent channelization. Water temperatures varied from 1° C in January to 30° C in July.

Twenty-three species of fishes occur at this site. The most common madtom at Mill Creek is *N. miurus*; *N. nocturnus* is less abundant but regularly present, and the tadpole madtom, *N. gyrinus*, is rarely captured.

Other species of fishes collected with the madtoms include *Canpostoma anomalum*, *Notropis lutrensis*, *Pimephales notatus*, *Semotilus atromaculatus*, *Erimyzon oblongus*, *Minytrema melanops*, *Moxostoma erythrurum*, *Ictalurus natalis*, *Fundulus olivaceus*, *Gambusia affinis*, *Aphredoderus sayanus*, *Lepomis cyanellus*, *L. megalotis*, *Pomoxis annularis*, *Etheostoma chlorosomum*, *E. gracile*, *E. procliare*, *E. squamiceps*, *Percina caprodes* and *P. maculata*. On one occasion a single specimen of a mudpuppy, *Necturus maculosus*, was collected with *N. nocturnus*.

METHODS

Methods of study followed Mayden and Burr (1981) except as noted. Observations and minnow seine collections were made at approximately one-month intervals from 27 August 1978 to 29 February 1980. During the breeding season observations were made more frequently. Additional observations and collections of breeding individuals were made in June 1981. In all, 145 specimens were preserved and examined. Most collections were made at night; observations of nesting were made during the day. Lengths throughout the text refer to standard lengths in millimeters (SL, mm); total length (TL) is used in the description of embryos and larvae. All aquarium-held pairs that spawned were injected with human chorionic gonadotropin (HCG) at 50 IU at a volume of 0.05 ml per injection.

HABITAT

During fall and winter, young occurred primarily in mixed gravel and sand riffles with accumulations of sticks, leaves, trash and other debris. Individuals were often common in the heads or bases of riffles where the current was strong. These riffles averaged

15 cm in depth and about 1.5 m in width. Adults were found primarily in riffles throughout most of the year but some were collected from mud-bottomed pools with *N. miurus*. During the breeding season (mid May thru July) adults were most common in shallow pools but often were in shallow riffles when the water velocity was greatly reduced.

Throughout its range, *N. nocturnus* characteristically is found in moderate to fast current over gravel or debris in medium-size to large streams. The water is frequently turbid but clear water is probably preferred (Taylor 1969).

REPRODUCTION

Reproductive Cycle of the Male

Testes of mature males were opaque white, had numerous finger-like projections of various sizes and were nearly identical in appearance to those illustrated or described for the margined madtom, *N. insignis* (Clugston and Cooper 1960: fig. 3B), the slender madtom *N. exilis*, and *N. miurus* (Burr and Mayden 1982, Mayden and Burr 1981).

Gonadosomatic indices (GSI) were recorded for specimens taken from August 1978 to July 1979. From August to May, GSI for males 1+ or greater in age remained about the same (\bar{X} GSI = 2.6, SD = 1.02, N = 11), but increased dramatically in June and July to a maximum of 9.1 (\bar{X} = 6.2, SD = 2.17, N = 10). Throughout the year, GSI for males less than 1 year old fluctuated little and averaged 2.2 (SD = 0.41, N = 13). A decrease in GSI for older males occurred after July at the end of the breeding season.

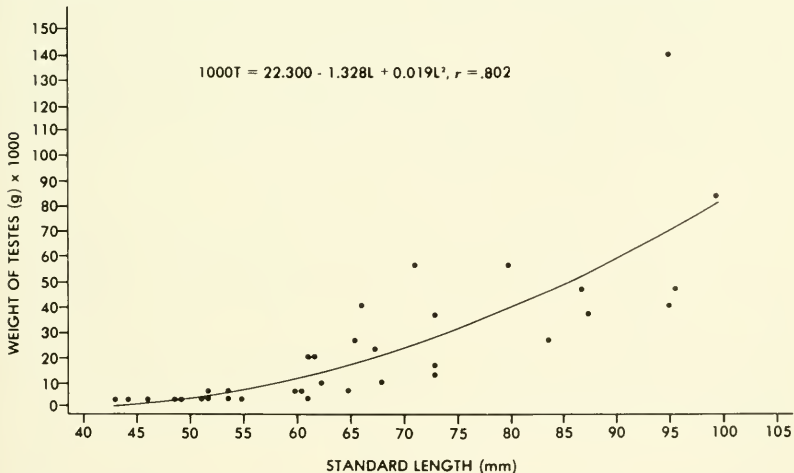


FIG. 1.—Relationship between weight of testes and standard length in 36 male *Noturus nocturnus* from Mill Creek.

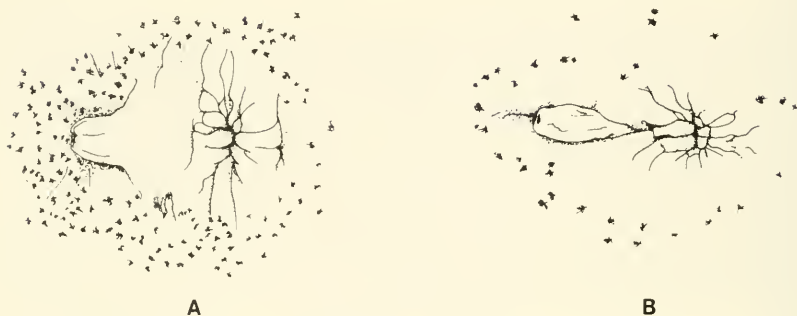


FIG. 2.—Genital papillae of *Noturus nocturnus* from Mill Creek. A) Breeding male 65.7 mm SL collected 19 June 1979; B) Breeding female 73.0 mm SL collected 22 June 1979. Right is anterior. 25 \times .

The relationship between weight of testes (T) and standard length (L) of males was curvilinear (Fig. 1), and was best depicted by the equation $1000 T = 22.300 - 1.328 L + 0.019 L^2$, with $r = 0.802$. Testis weight was negligible until the male exceeded 60 mm SL or 15 months of age.

As in other *Noturus*, breeding males developed swollen lips, genital papillae (Fig. 2A) and epaxial muscles on the head between May and July. Nonbreeding males did not develop these features and were similar in appearance to females. Appearance of the genital papilla was useful in distinguishing the sexes of individuals 1+ or greater in age, especially from May to July. Coloration of males did not change with the breeding season and was as described by Taylor (1969).

As judged by primary and secondary sexual characteristics and nesting males captured, sexual maturity of males is probably attained in the third summer of life (2 years old). This is similar to what has been reported for other long-lived species of *Noturus* (Clugston and Cooper 1960, Burr and Maiden 1982, Maiden et al. 1980, Maiden and Burr 1981).

Reproductive Cycle of the Female

As indicated by shape and size of the genital papillae (Fig. 2B), the GSI (Fig. 3) and degree of abdominal distention, females began to prepare for spawning in May and were ripe with mature oocytes through July. Breeding females were similar in color to males, but did not develop swollen head muscles and lips. The genital papillae of females were swollen from May to July, but differed from those of breeding males by being more conical, and partially concealed anteriorly by the swelling of adjacent tissues (Fig. 2B).

Relative ovary weights exhibited little variation from August

to May, but increased markedly to higher levels in June and July (Fig. 3). In June and July, GSI ratios ranged from 20 to 90 ($\bar{X} = 56.7$) in the seven females represented in Table 1. In June, the GSI of 40 was of a spent female and in July, the GSI of 21 and 20 were of partially spent and immature females, respectively. The mean GSI for females in June and July, excluding spent and immature individuals, was 79.0. The proportionally largest ovaries (equalling 9.0% of adjusted body weight) occurred in a 1-year-old, 69-mm female collected 30 July 1979. In contrast, ovaries represented 24.8 percent of adjusted body weight in breeding females of *N. miurus* from Mill Creek (Burr and Maiden 1982). From August to April, oocytes of females were small (averaging 1.0 mm) and whitish in color. During the breeding season, two size classes of oocytes were evident in mature females ($N = 10$); smaller, white oocytes that averaged 0.8 mm and orange, mature oocytes that averaged 2.0 mm (range = 1.8–2.3 mm).

The few 1- and 2-year old females collected from May to July had large, mature oocytes and apparently would have spawned

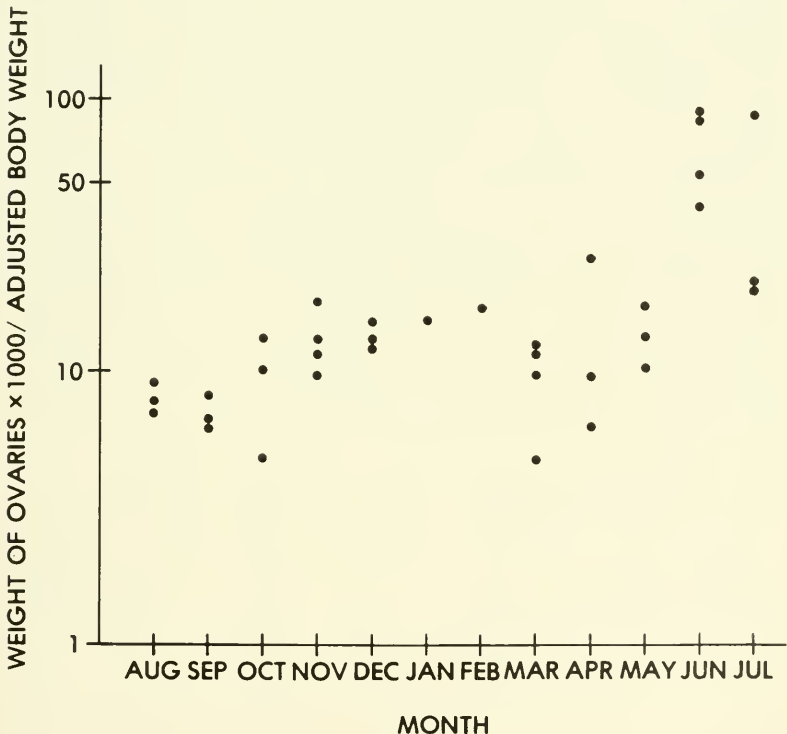


FIG. 3.—Monthly variations in ovarian weight relative to adjusted body weight of 35, 2- to 52-month old female *Noturus nocturnus* from Mill Creek. The vertical axis is a logarithmic scale.

(those collected in May spawned in aquaria in mid-June). Except for young-of-the-year collected in July, no nonbreeding females were collected from May to July. In five mature females ranging in size from 67 to 75 mm, and collected during June and July, the number of mature oocytes ranged from 85 to 116 ($\bar{X} = 102.2$; Table 1). Ripe *N. miurus* and *N. exilis* females averaged 66.2 and 83.6 mature oocytes, respectively (Burr and Mayden 1982, Mayden and Burr 1981). Small samples of *N. nocturnus* prevented meaningful comparisons between number of mature oocytes and age, length and weight of the female.

Nesting

The first evidence of nesting *N. nocturnus* in Mill Creek was the discovery of a male in a narrow-mouthed glass bottle on 9 May 1979. On 17 May 1979, a male and female in breeding condition were found in a 355 ml beer can. Neither of these nesting sites contained embryos or larvae, but the pair spawned 102 eggs in an aquarium on 18 June 1979, following several injections with human chorionic gonadotropin. On 22 June 1979, two other aquarium-held pairs, injected with HCG, spawned 35 and 40 eggs, respectively.

Several additional visits to Mill Creek during the summer of 1979 resulted in the discovery of *N. miurus* nests containing embryos or larvae (Burr and Mayden 1982), but only males of *N. nocturnus* were found in beer cans or bottles.

On 25 June 1981, three nests of *N. nocturnus* were found, all in 355 ml beer cans and each containing a clutch of embryos. The nests were located in a shaded area of the creek with some current, about 0.5 m wide and about 10–15 cm deep, where the water temperature was 25° C. Four other solitary males in breeding condi-

TABLE 1. Relationship between size, age and ovary weight of *Noturus nocturnus* females and the number of mature oocytes.

SL, mm	Adjusted body weight ^a (g)	Month of collection	Age in Months	Weight of ovaries (g)	Number of mature (orange) oocytes	GSI ^b
62	3.45	June	12	0.18	94	52
63	4.17	June	12	0.37	115	89
65	4.15	June	12	0.17	16	40
75	5.90	June	24	0.50	116	85
68	5.64	July	13	0.12	85	21
69	5.58	July	13	0.50	101	90
69	5.36	July	13	0.12	—	20

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

^b Equals (weight of ovaries \times 1000)/adjusted body weight.

tion were found in 355 ml beer cans, evidently in preparation for spawning. Numerous pairs of *N. miurus* were found in beer cans but only one nest contained a single male with embryos. Nest cans of *N. nocturnus* usually contained some tightly packed mud or silt against the bottom. Similar to *N. miurus*, *N. nocturnus* probably nests under rocks but, due to the turbidity of Mill Creek, we were unable to search these areas.

As in other species of *Noturus* we have studied (*albater*, *elegans*, *exilis*, *flavater*, *flavus*, *miurus*), embryos adhered to each other in a roundish mass but not to other surfaces. Embryos were spherical and lemon-yellow.

All males found in beer cans were 2 or 3 years old and like nesting males of other species of *Noturus* had empty stomachs. Nesting males were 73.0, 75.3 and 75.4 mm SL, and had 154, 139, and 47 eggs in their nests, respectively. The clutch of 47 embryos may have only been partially complete, since females of some species of *Noturus* probably lay at least two clutches of eggs per year (Mayden and Burr 1981).

Unlike other madtoms, breeding male and female *N. nocturnus* developed numerous abrasive, tiny, white structures over their heads and bodies. Histological preparations of skin of both breeding and nonbreeding males revealed that these structures were taste buds. The roughness of the taste buds during the nesting season and the close contact maintained in the nesting situation between males and females suggests that these structures might be analogous to breeding tubercles and serve as a stimulus to courtship or spawning.

As stated earlier, the heads of adult males become swollen during the breeding season and increased in both width and depth. Head width in 10 breeding males ranged from 18.5–26.5 mm ($\bar{X} = 21.7$) and head depth ranged from 11.1–15.9 mm ($\bar{X} = 13.3$). 'Pop-top' beer and soda can openings ranged from 18.5–28.0 mm in length ($\bar{X} = 23.7$) and 13.0–20.0 mm in width ($\bar{X} = 16.2$). Thus, there was little room to spare at the opening of a can once a male was inside and in his characteristic position. As judged from aquarium-held individuals, breeding males typically faced the opening of the can, blocking entry of virtually all potential predators.

Pflieger (1975) reported female *N. nocturnus* with fully developed eggs from the last week of May in Missouri and suggested that the species spawns in spring or early summer. At the latitude of southern Missouri and southern Illinois we have found eight species of madtoms nesting only in late June and July. It is unlikely that any madtom spawns in the spring in this region.

The spawning and nesting season for *N. miurus* and *N. nocturnus* overlaps considerably from mid-June to late July in Mill Creek. Because most breeding pairs or individuals of both species that

we observed use cans or bottles for nests, there may be some competition for nest sites between the two species.

DEVELOPMENT

On 18 June 1979, a freshly-laid clutch of *N. nocturnus* eggs was removed from a nesting pair that had spawned in a 355 ml beer can in an aquarium. Egg diameters ranged from 3.6 to 4.5 mm (\bar{X} = 3.9, N = 5); yolk diameters ranged from 3.1 to 4.0 mm (\bar{X} = 3.3, N = 6).

Of the clutch of 102 eggs, 60 were incubated in a culture dish and the remaining were returned to the parent nest where they were later consumed by the parents. At 25° C, eggs hatched in 139–161 hr (5.8–6.7 days), a shorter developmental time than *N. exilis* and *N. miurus*. At 25° C, *N. exilis* hatched in 187–210 hr; *N. miurus* hatched in 189–215 hr (Mayden and Burr 1981, Burr and Mayden 1982). Based on the 60 eggs, hatching success was 100 percent.

Hatchlings (Fig. 4A) ranged from 7.5 to 8.0 mm TL (\bar{X} = 7.7, N = 3), had a few scattered melanophores on top of the head and heavily pigmented eyes. All fins were formed but only the caudal fin showed any differentiation of rays. Three pairs of rudimentary barbels were present. *N. nocturnus* hatchlings were virtually identical in appearance to those of *N. exilis* (Mayden and Burr 1981: fig. 17C and D) and *N. miurus* (Burr and Mayden 1982: fig. 4A).

One-day-old larvae ranged from 9.7 to 10.8 mm (\bar{X} = 10.1, N = 4), had more melanophores concentrated on the top of the head and had rays differentiated in all fins. Four pairs of barbels were present.

Four-day-old larvae ranged from 10.7 to 11.5 mm TL (\bar{X} = 11.1, N = 2) and were beginning to appear adult-like in their physiognomy. The body shape at this age and size is stockier than *N. exilis* and *N. miurus* of about the same size and age (Mayden and Burr 1981: fig. 18C and D, Burr and Mayden 1982: fig. 4B). Melanophores were sparse but evenly distributed over the head and body, and an early, open cephalic lateral-line canal was present. Spines were partially developed in the pectoral and dorsal fins. Over one-half the yolk sac was absorbed (Fig. 4B).

At eight days, larvae ranged from 11.7 to 12.9 (\bar{X} = 12.3, N = 5) and had large melanophores concentrated over the head and body. The yolk sac was over three-fourths absorbed and the cephalic lateral-line system was partially closed (Fig. 4C).

At 15 days, larvae ranged from 14.8 to 15.5 (\bar{X} = 15.0, N = 3) and had melanophores distributed over the head, body and fins in a pattern like that of an adult. The yolk sac was completely absorbed and the overall morphology was adult-like (Fig. 4D).

The smallest specimen collected by seine from Mill Creek was an 11.8 mm SL individual taken in July. This individual had the yolk sac absorbed but was not as darkly pigmented as some 15-day-old laboratory-reared individuals.

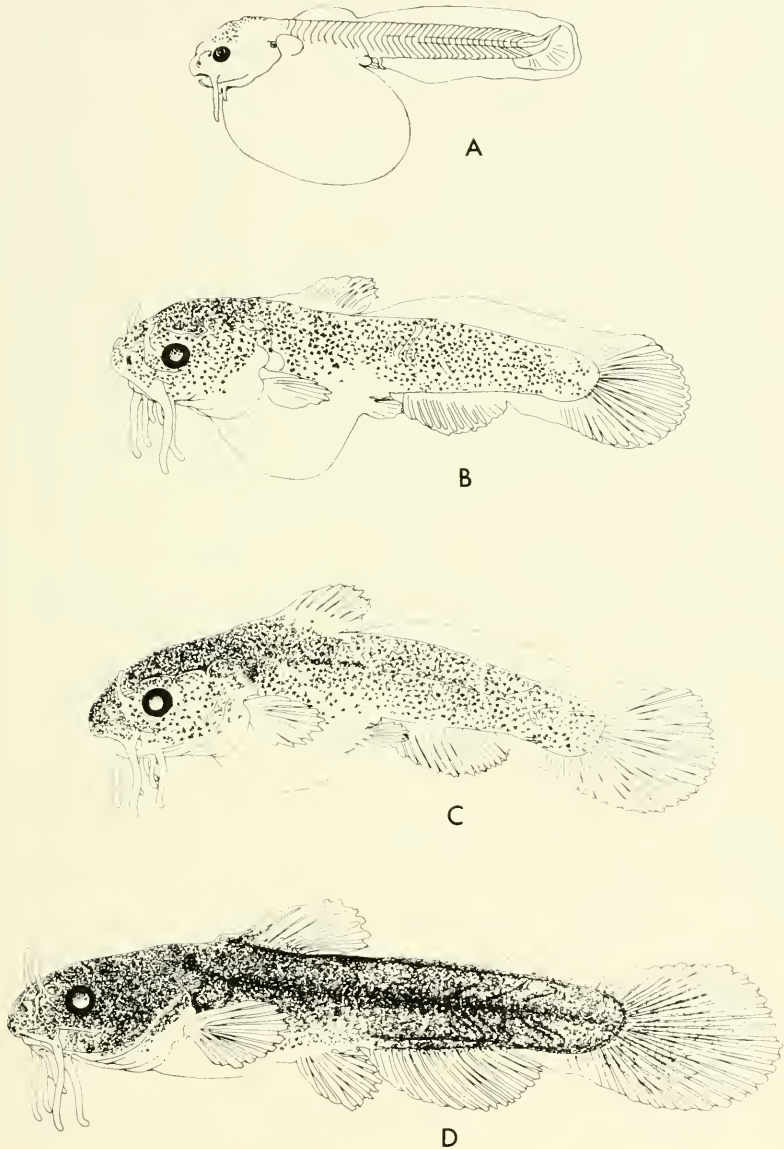


FIG. 4.—Representative stages of development in *Noturus nocturnus* from Mill Creek. A) Hatchling, 7.9 mm TL; B) 4-day-old larva, 11.5 mm TL; C) 8-day-old larva, 12.4 mm TL; D) 15-day-old larva, 14.1 mm TL. 25 \times .

GROWTH

Rate of increase in length declined with age; half of the first year's growth was attained in about eight weeks (Fig. 5). The relationship between standard length (Y) and age in months (X) for males was $Y = 18.776 + 43.434 \text{ Log } X$, with $r = 0.923$, and for females was $Y = 16.830 + 43.409 \text{ Log } X$, with $r = 0.894$. Males and females grew at nearly the same rate in length, but males lived slightly longer (54 versus 52 months). From 13 to 18 months males ($N = 6$) averaged 40.7 mm and females ($N = 5$) averaged 38.5 mm. From 19 to 24 months males ($N = 6$) averaged 55.6 mm and females ($N = 5$) averaged 50.5 mm. At 25 to 30 months males ($N = 4$) averaged 64.7 mm and females ($N = 4$) averaged 66.1 mm. Beyond these ages, sample sizes were too small to be meaningful. The largest specimen collected from Mill Creek was a 101.5 mm female collected 27 October 1979 that weighed 19.6 g. The largest male, collected 28 December 1979, was 99.2 mm and weighed 17.5 g. The largest specimen Taylor (1969) examined was 121.5 mm SL from Missouri. We found a 122.6 mm SL individual from Nolin Reservoir, Kentucky (specimen at University of Louisville). Taylor (1969) stated that most specimens of *N. nocturnus* were under 100 mm SL and that the Missouri specimen was an exceptionally large one.

Adjusted body weight increased at a constant rate for both sexes; one half of the first year's mean body weight was reached in about three months for both sexes (Fig. 6). The relationship be-

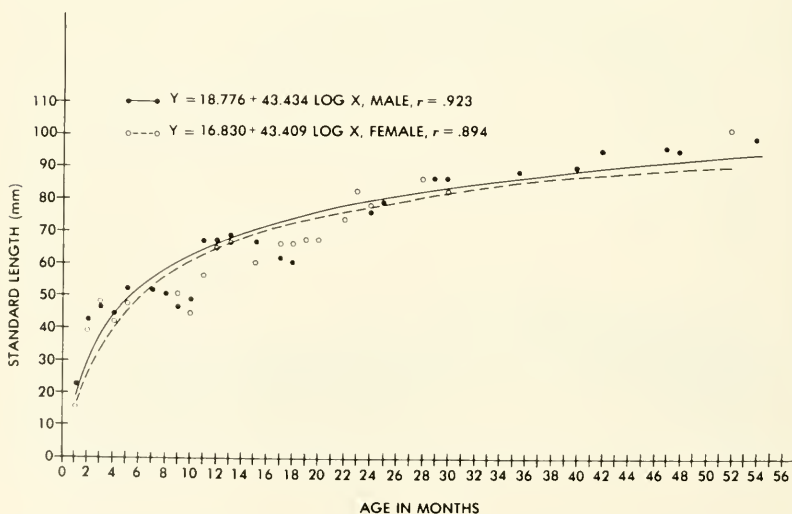


FIG. 5.—Growth in standard length of 145 *Noturus nocturnus* collected from Mill Creek. Dots represent means for males; circles represent means for females.

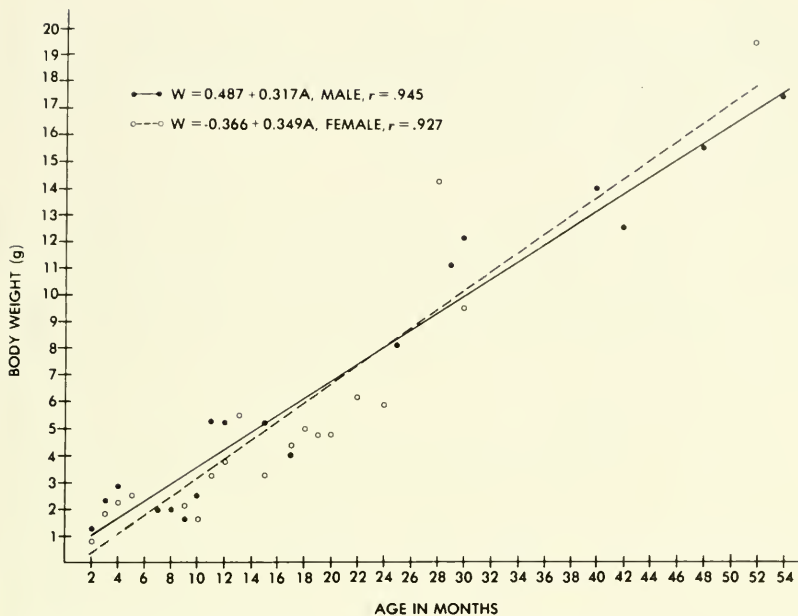


FIG. 6.—Growth in adjusted body weight of 71 *Noturus nocturnus* from Mill Creek. Dots represent means for males; circles represent means for females.

tween adjusted body weight (W) and age in months (A) for males was $W = 0.487 + 0.317 A$, with $r = 0.945$, and for females was $W = -0.366 + 0.349 A$, with $r = 0.927$. Linear growth equations for body weight did not differ significantly between the sexes.

DEMOGRAPHY

Composition

Of the 145 *N. nocturnus* collected in Mill Creek between 27 August 1978 and 25 June 1981, 61.4 percent were up to 1 year old, 22.8 percent were between 1 and 2 years old, 10.3 percent were between 2 and 3 years old and 5.5 percent were 3 years or older (Table 2).

TABLE 2. Distribution of sexes and year classes in samples of *Noturus nocturnus* from Mill Creek.

Sex	Number by Year Class					Total
	0	1+	2+	3+	4+	
Males	43	19	10	5	2	79
Females	46	14	5	0	1	66
Total	89	33	15	5	3	145

There was no significant ($\alpha = 0.05$) deviation from a 1:1 sex ratio in the first (0) or second (1+) year class. Sampling was biased toward males in older age classes, particularly during the nesting season, thus a meaningful comparison of the sex ratio of older age classes was not possible.

Survival

Of the 79 males collected 54.4 percent were up to 1 year old, 24.1 percent were between 1 and 2 years old, 12.7 percent were between 2 and 3 years old and 8.9 percent were 3 years or older. Of the 66 females collected 69.7 percent were up to 1 year old, 21.2 percent were between 1 and 2 years old, 7.6 percent were between 2 and 3 years old and 1.5 percent were 3 years or older (Table 3).

Males lived slightly longer than females in Mill Creek. The oldest male was 54 months collected in December, the oldest female was 52 months collected in October. Males and females of *N. miurus* lived as long as 36 and 25 months, respectively, in Mill Creek (Burr and Mayden 1982). *Noturus exilis*, *N. flavus*, *N. gyrinus* and *N. insignis* all live at least 4 years (Mayden and Burr 1981, Scott and Crossman 1973, Mahon 1977, Clugston and Cooper 1960).

DIET

An examination of 41 stomachs of *N. nocturnus* from all seasons of the year (Table 4) revealed that aquatic insect larvae were the

TABLE 3. Relative survival of year classes of *Noturus nocturnus* in Mill Creek expressed as proportions of the 0 year class ($1 \times^1$), the 1+ year class ($1 \times^2$), the 2+ year class ($1 \times^3$) and the 3+ year class ($1 \times^4$).

Sample	Year Class	Number of Specimens	Survival			
			$1 \times^1$	$1 \times^2$	$1 \times^3$	$1 \times^4$
Males	0	43	1.000	—	—	—
	1+	19	.442	1.000	—	—
	2+	10	.233	.526	1.000	—
	3+	5	.116	.263	.500	1.000
	4+	2	.047	.105	.200	.400
Females	0	46	1.000	—	—	—
	1+	14	.304	1.000	—	—
	2+	5	.109	.357	1.000	—
	3+	0	.000	.000	.000	1.000
	4+	1	.022	.071	.200	.000
Total Sample	0	89	1.000	—	—	—
	1+	33	.371	1.000	—	—
	2+	15	.112	.455	1.000	—
	3+	5	.056	.152	.333	1.000
	4+	3	.034	.091	.200	.600

TABLE 4. Stomach contents of *Noturus nocturnus* from Mill Creek by season. Figures in parentheses are numbers of stomachs examined.

Food Organism	Percent of Stomachs in Which Food Organism Occurred				Mean Number of Food Organisms Per Stomach			
	Summer (10)	Fall (11)	Winter (8)	Spring (12)	Summer (10)	Fall (11)	Winter (8)	Spring (12)
Nematoda	10.0	-	12.5	-	0.10	-	0.38	-
Annelida								
Oligochaeta	-	9.0	-	-	-	0.09	-	-
Arachnida								
Araneae	-	9.0	-	-	-	0.09	-	-
Crustacea								
Amphipoda	-	-	-	8.3	-	-	-	0.08
Isopoda								
<i>Lirceus</i>	-	-	-	41.7	-	-	-	0.42
<i>Asellus</i>	-	27.3	-	-	-	0.27	-	-
Decapoda								
<i>Orconectes</i>	20.0	-	-	8.3	0.20	-	-	0.08
Insecta								
Ephemeroptera	70.0	36.4	37.5	16.7	2.60	0.64	0.38	0.17
Odonata	10.0	-	-	-	0.10	-	-	-
Trichoptera	40.0	45.5	50.0	58.3	0.50	1.64	0.88	1.00
Coleoptera								
Elmidae	-	9.0	-	-	-	0.09	-	-
Diptera								
Simuliidae	-	18.2	50.0	8.3	-	0.73	8.25	0.08
Chironomidae	60.0	63.6	50.0	41.7	3.90	1.18	1.88	0.92
Unident. pupae	-	9.0	-	-	-	0.09	-	-

predominant food items. Ephemeropterans, trichopterans, and chironomid larvae made up the bulk of the diet and were consumed during all seasons of the year; simuliids were eaten during the fall, winter and spring. Crustaceans, nematodes, oligochaetes, and arachnids made up only small portions of the diet (Table 4).

In Kansas, *N. nocturnus* from the Arkansas River system is reported to eat insects, insect larvae and small crustaceans (Cross and Collins 1975). Clark (1978) in her unpublished Masters thesis reported that the stomachs of three *N. nocturnus* captured in April, 1977, from Black Creek, Mississippi, contained the remains of three speckled madtoms, *Noturus leptacanthus*.

PARASITISM

Hoffman (1967) did not list any parasites of *N. nocturnus*. The only endoparasite found during examination of stomach contents was the fluke *Crepidostomum* (in four specimens). The ectoparasitic copepod *Lernaea* was found on two specimens, one from June and one from July.

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SUMMARY

The life history of *Noturus nocturnus* was studied at Mill Creek, Pulaski County, Illinois, between 27 August 1978 and 25 June 1981. A total of 145 specimens from 1 to 54 months in age was collected. Males were sexually mature at 2 years; those found in nests ranged

in size from 67.0 to 75.4 mm SL. Females had mature oocytes from late May through July; some females reached sexual maturity by 1 year of age. The number of mature oocytes produced by a female ranged from 85 to 116 ($\bar{X} = 102.2$). Three nests, each containing a single clutch of eggs and guarded by a single male, were found in 355 ml beer cans in shaded, narrow riffles with reduced flow on 25 June 1981, at a water temperature of 25° C. Clutch sizes were 47, 139 and 154; eggs were spherical and lemon-yellow in color and ranged in diameter from 3.6 to 4.5 mm. Eggs incubated in the laboratory at 25° C hatched in 139–161 hr with a hatching success of 100 percent. Individual freckled madtoms grew in length at a decreasing rate and in body weight at a constant rate for at least 4 years. One-half of the first year's mean growth in length was reached in about 8 weeks; about 12 weeks was required to attain one-half of the first year's mean body weight. Ephemeropteran, trichopteran and chironomid larvae were consumed during all seasons of the year and made up the bulk of the diet in 41 stomachs examined.

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