

BIOLOGY OF THE STONECAT, *NOTURUS FLAVUS* (SILURIFORMES: ICTALURIDAE), IN CENTRAL ILLINOIS AND MISSOURI STREAMS, AND COMPARISONS WITH GREAT LAKES POPULATIONS AND CONGENERS¹

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ABSTRACT. Aspects of the general biology of the stonecat, *Noturus flavus*, were analyzed from 261 preserved specimens from Illinois and Missouri streams. Individuals ranged in age from one to 62 mo. The largest specimens examined were a 180-mm SL male and a 165-mm SL female. Females were mature at 3-4 yr and a mean SL of 119.4 mm. Mature oocytes, produced seasonally, ranged from 189 to 570 (\bar{x} = 377.8; N = 12) per female. Seven nests, each containing a clutch of embryos or larvae and guarded by a male, were found under large, flat rocks in pools and riffles. All nest-guarding males were 3 yr old and ranged from 87 to 105 mm SL (\bar{x} = 94.8). Nests were observed in early July at water temperatures of 27 to 29°C. Clutch sizes ranged from 104 to 306+; embryos were spherical, opaque white or light yellow, and ranged in diameter from 2.6 to 4.0 mm (\bar{x} = 3.4 mm; N = 40). At hatching, mesolarvae ranged from 6.7 to 7.5 mm TL; development was similar to that described for other ictalurids. Stomachs of adults contained a variety of benthic organisms, primarily aquatic larval insects and decapod crustaceans.

Great Lakes stonecats live longer, attain a greater maximum size, and have a higher absolute fecundity than southern inland stream populations. Comparisons with congeners indicate that *N. flavus* has life-history traits that are near one extreme within the genus, and they include a longer lifespan and a lower relative fecundity.

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INTRODUCTION

The ictalurid catfish genus *Noturus* contains 25 described species, all endemic to eastern North America. Systematics of the genus were revised by Taylor (1969). Two species have been described since publication of his monograph: *Noturus taylori* Douglas 1972 and *Noturus stanauli* Etnier and Jenkins 1980. Aspects of the biology of nearly half of the species recently have been reported (Mahon 1977, Clark 1978, Mayden et al. 1980, Burr and Dimmick 1981, Mayden and Burr 1981, Miller 1984, Burr and Mayden 1982a, b, 1984,

Dinkins 1984, Shute 1984, Mayden and Walsh 1984). The present study considers the general biology of the stonecat, *Noturus flavus* Rafinesque, in Illinois and Missouri streams. Comparisons are made with published studies of *N. flavus* in Lake Erie, and the reproductive biology of the species is compared with congeners. Brief accounts of certain aspects of the biology of this species were presented by Eigenmann 1896, Greeley 1929, 1934, Bowman 1936, Langlois 1954 (nesting sites, spawned eggs, fecundity), Fish 1932, Tin 1982 (larval development), Cahn 1927, Greeley 1929, Bowman 1936, Gilbert 1953, Langlois 1954, Pflieger 1975, Wolfert et al. 1975, Angermeier 1982 (diet), Gilbert 1953 and Carlson 1966 (age and growth).

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Throughout most of its range in north-central United States and southern Canada (Taylor 1969: map 8), *N. flavus* generally inhabits riffles of medium-size to large streams that usually have many large rocks; it is also present in lakes (e. g., western Lake Erie) around limestone reefs and gravel shoals where the currents and wave action produce stream-like conditions (Trautman 1981). *N. flavus* also lives in the main channels of the Missouri, Ohio, and Mississippi rivers, where small-eyed individuals are found over sand in swift current (pers. observ., Pflieger 1975).

METHODS AND MATERIALS

Laboratory procedures generally followed those of Mayden et al. (1980), Mayden and Burr (1981), and Burr and Mayden (1982a, b). Analyses of size, age, growth, reproductive cycles, sex ratios, diet, and parasites were made from 261 preserved specimens from central Illinois and Missouri streams. Locality data of sites where specimens were collected are available from the authors. Additional specimens were collected and field observations were made of nest sites, embryos, and larvae at Meramec River, Meramec River State Park, Franklin Co., Missouri (16 July 1981, 1982), and Middle Fork Vermilion River, south of Potomac, Vermilion Co., Illinois (8 July 1982). Adults were collected with seines and dip nets; embryos and larvae were captured with dip nets while using snorkeling gear. Voucher specimens examined in this study are deposited at Southern Illinois University at Carbondale and the Illinois Natural History Survey, Champaign.

Adults were measured to the nearest mm standard length (SL) with dial calipers and were aged by counting annual rings on cross sections of pectoral spines following the procedures of Clugston and Cooper (1960) as modified by Mayden and Burr (1981). Some specimens with excessively pliable fin spines were aged by counting annuli on vertebrae. Adjusted body weights (weight of specimen minus stomach, intestine, liver, and gonads) were measured to the nearest 1.0 mg. Gonads were blotted dry, and their weights were recorded to the nearest 1.0 mg and used to calculate the gonadosomatic index (GSI) by the formula $GSI = \frac{\text{weight of gonads (g)}}{\text{adjusted body weight (g)}} \times 1000$. Oocyte diameters and total lengths (TL) of larvae were measured to the nearest 0.1 mm with an ocular micrometer. Developmental stages of embryos and larvae were approximated from times reported for laboratory-reared *N. albatel*, *N. exilis*, *N. miurus*, and *N. nocturnus* at 25°C (Mayden et al. 1980, Mayden and Burr 1981, Burr and Mayden 1982a, b) and from larvae of one laboratory-reared clutch of *N. flavus* preserved at various intervals. Drawings of larvae were done with the aid of a camera lucida at

magnifications of 75-350×. Terminology for intervals of larval stages follows Snyder (1976).

RESULTS

AGE, MAXIMUM SIZE, AND WEIGHT-LENGTH REGRESSION. Only some breeding and exceptionally large individuals were aged in this study. Specimens (90-135 mm SL; N = 17) aged from pectoral spines were probably three or four yr old. The largest specimens, aged from vertebrae, were a 165-mm female (4+ yr), a 175-mm male (5+ yr), and a 180-mm male (5+ yr) (Illinois: Vermilion Co., Stony Creek, 21 Sept. 1951). The largest specimen from the Vermilion River was a 131-mm female (3+ yr; 28 July 1964); from the Meramec River it was a 136-mm male (age undetermined; 16 July 1981).

Growth rate was greatest in the first year. In early August 1964, 17 one-yr-old specimens from the Vermilion River averaged 48.6 mm, close to the mean of 52.5 mm reported for one-yr-old specimens from Ohio streams (Gilbert 1953). Seven three-yr-olds had a mean SL of 100.0 mm. Ten four-yr-olds averaged 123.3 mm, differing from an average SL of 104 mm for Ohio stream specimens of the same age (Gilbert 1953). Lack of adequate sample sizes in this study did not allow clear separation of age classes by length-frequency analysis.

Regression of body weight on length of Illinois specimens was similar to that found in South Dakota and Ohio specimens. There was no significant difference in weight-length regression equations between males and females; for the sexes combined, the relationship between adjusted body weight in grams (W) and SL was $\text{Log } W = -4.91 + 3.04 \text{ Log } \text{SL}$ ($r = 0.99$; N = 132). Slope values of 2.84 and 3.05 were reported for Ohio (N = 68) and South Dakota (N = 47) specimens, respectively (Gilbert 1953, Carlson 1966). The former study included Lake Erie specimens, the latter used total lengths, and both presumably used total body weights; all may be possible reasons for the slight differences in slope and intercept values from those in this study.

AGE AND SIZE AT MATURITY. Females from Illinois reached reproductive maturity in a minimum of three yr, in contrast to smaller madtoms such as *N. exilis* and *N. nocturnus* that mature in one-two yr (Mayden and Burr 1981, Burr and Mayden 1982b). Mature females ranged in size from 97-134 mm (\bar{x} = 119.4 for two three- and 10 four-yr-olds). Several collections had gravid and immature females of similar sizes, indicating overlap in size of females possibly of different ages, or that some individuals may not breed for the first time until their fourth yr. No female older than five yr was seen, despite studies indicating that the species lives much longer than other madtoms (Gilbert 1953, Carlson 1966).

Age at first spawning for males could not be ascertained, although all males found guarding nests were three yr old and greater than 85 mm (\bar{x} = 94.8 mm; table 1).

REPRODUCTIVE CONDITION. A. Males. In gross appearance, testes of *N. flavus* were opaque white and fimbriate as in other ictalurids (Sneed and Clemens 1963, Mayden and Burr 1981). Weight of testes was positively correlated with increased body weight. For combined monthly samples of immature and mature males, linear regression of testes weight in milligrams (T) on adjusted body weight in grams (W) was $T = -7.9 + 2.2W$ ($r = 0.82$; $N = 55$). Growth of testes relative to increasing SL was curvilinear, $T = 33.2 - 1.3 SL + 0.01 SL^2$ ($r = 0.84$; fig. 1).

There was slight seasonal variation in GSI of males from May through September. Peak reproductive activity was indicated by an increase in mean GSI for all males per sample from a minimum in May of 0.3 to a maximum of 1.2 and 1.4 in June and July, respectively. The largest relative testes weight (equalling 0.6% adjusted body weight) was that of a 97.4-mm specimen collected 4 June.

As in other species of the genus, there was no marked sexual dimorphism outside of the breeding season. Nuptial males of *N. flavus* had enlarged cephalic epaxial

muscles and swollen genital papillae (fig. 2).

B. Females. From late spring to early autumn there was little change in GSI of immature females (fig. 3), with a slight decrease from a mean of 4.4 ($N = 3$) in May to 2.4 ($N = 17$) in September. Lack of specimens from the remainder of the year prevented a comparison of GSI throughout winter and early spring, but ovarian growth in immature *N. flavus* is probably similar to the variable, slight seasonal increase in other species (Mayden and Burr 1981, Burr and Mayden 1982a, b). GSI of immature females reached a minimum in August (\bar{x} = 2.2; $N = 17$), possibly due to the inclusion of more young (0 and 1+ yr classes) specimens having very small ovaries, and to increased somatic growth during summer.

GSI of mature females increased in late spring, corresponding to accelerated ovarian recrudescence and oocyte vitellogenesis (fig. 3). Maximum ovarian mass and peak spawning condition were attained in females collected from the Rock, Sangamon, and Vermilion river drainages, Illinois, from 4 June to 28 July. Twelve gravid females had a mean adjusted body weight of 24.9 g (range = 14.2-40.4 g) and a mean ovarian weight of 3.7 g (range = 1.8-6.4 g). Mean GSI of prespawning females increased from 115.9 ($N = 8$) in June to 202.4 ($N = 5$) in July. The proportionally heaviest ovaries (equalling 29.3% adjusted body weight) were those of a 122-mm female collected from the Vermilion River on 8 July 1982. Mean GSI ratios from gravid females of other medium-size to large madtoms collected from May through July were: 79 ($N = 4$) in *N. nocturnus* (Burr and Mayden 1982b), 107 ($N = 7$) in *N. flavater* (Burr and Mayden 1984), 145 ($N = 12$) in *N. miurus* (Burr and Mayden 1982a), and 211 ($N = 11$) in *N. exilis* (Mayden and Burr 1981).

Externally, gravid females appeared similar to immature specimens except in having greatly distended abdomens and swollen genital papillae (fig. 2).

TABLE 1

Nesting variables and size and age of young N. flavus from Meramec River, Missouri, and Middle Fork Vermilion River, Illinois. Estimates of post-hatching ages were based on laboratory-reared N. flavus; pre-hatching ages were estimated from times reported for other species of Noturus at similar stages of development.

Locality and date	Habitat	Length, width and thickness of nest cover (cm)	Water depth (cm) and water temperature (°C)	Size (mm SL) and age (years) of guardian male	No. of embryos or larvae collected	Approximate age in development	Size of embryos (mm) or larvae (mm TL). Mean and range (N)
Meramec River 16 July 1981	Crest of riffle	46:23:13	53:28.5°	96:3	50 mesolarvae (brood incomplete)	5 days post-hatching	10.5 9.7-11.1 (15) 3.5 3.3-3.7 (10) 2.9 2.6-3.1 (20) 7.0 (5) 11.2 (20) 12.9 (20)
Meramec River 16 July 1981	Crest of riffle	30:25:10	66:28.5°	105:3	180 embryos (brood complete)	10 h	3.3-3.7 (10) 2.9 2.6-3.1 (20) 7.0 (5) 11.2 (20) 12.9 (20)
Meramec River 16 July 1982	Pool	53:43:25	117:27.5°	93:3	208 embryos (brood complete)	ca. 24 h	2.9 2.6-3.1 (20) 7.0 (5) 11.2 (20) 12.9 (20)
Meramec River 16 July 1982	Pool	36:18:14	117:27.5°	87:3	104 mesolarvae (brood complete)	hatchlings	6.7-7.5 (5) 11.2 (20) 12.9 (20)
Meramec River 16 July 1982	Pool	31:28:8	117:27.5°	93:3	35 metalarvae (brood incomplete)	6 days post-hatching	10.9-11.5 (20) 12.9 (20)
Meramec River 16 July 1982	Pool	46:25:10	117:27.5°	...	306 metalarvae (brood incomplete)	9 days post-hatching	11.8-14.1 (20) 3.8 3.5-4.0 (10)
Vermilion River 8 July 1982	Riffle	61:31:8	25:27.5°	...	206 embryos (brood complete)	40-50 h	3.5-4.0 (10)

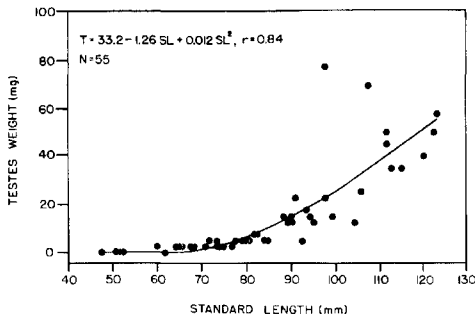


FIGURE 1. Relationship between testes weight and SL of *N. flavus*.

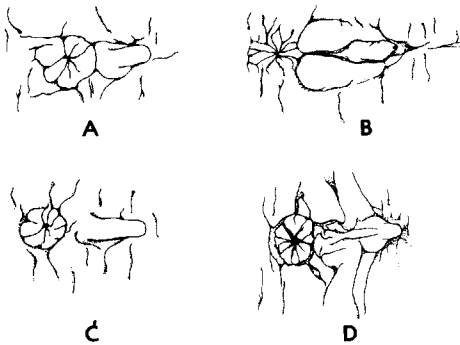


FIGURE 2. Genital papillae of *N. flavus*. A) 110-mm SL nonbreeding male, 21 Sept. 1951, Stony Fork, Illinois. B) 133-mm SL breeding male, 16 July 1981, Meramec River, Missouri. C) 144-mm SL nonbreeding female, same as A. D) 121-mm SL breeding female, 8 July 1982, Middle Fork Vermilion River, Illinois. Left is anterior.

OOCYTE DIAMETER AND FECUNDITY. Ovaries of gravid females contained two size-classes of oocytes as in congeners (Clark 1978, Mayden and Burr 1981). Large, vitellogenic oocytes were amber, ranged in diameter from 1.9 to 3.4 mm ($\bar{x} = 2.7$ mm; $N = 240$), and were assumed to be the only oocytes spawned during one season. Immature oocytes were small (less than 1.0 mm) and opaque white. In 12 gravid females from Illinois there was a significant positive correlation ($r = 0.86$) between mean oocyte diameter in mm (D) and increasing GSI, with $D = 1.99 + 0.005$ GSI (fig. 4).

Vitellogenic oocytes in gravid females ranged in number from 189 to 570

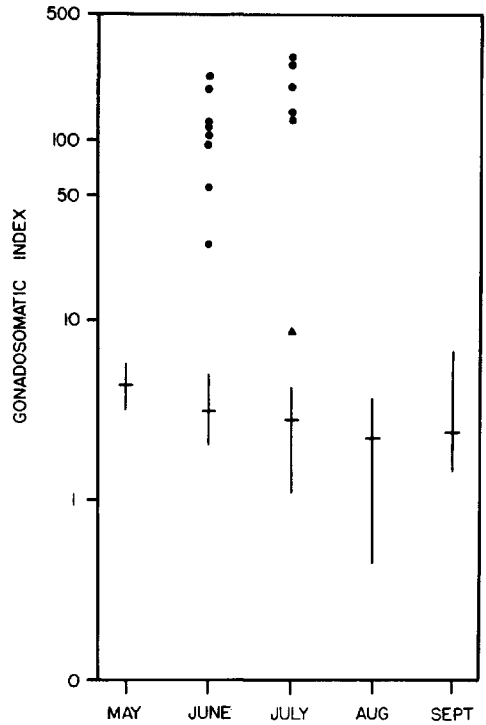


FIGURE 3. Summer variation in GSI of 77 female *N. flavus* from Rock, Sangamon, and Vermilion River drainages, Illinois. Vertical lines are sample ranges and horizontal lines are means for immature specimens; solid circles represent pre-spawning individuals; solid triangle partially spent female.

($\bar{x} = 377.8$; $N = 12$). Two females had considerably more oocytes in the left ovary than in the right [357 total, $P(\chi^2 \geq 1.72) > 0.25$; 570 total, $P(\chi^2 \geq 1.70) > 0.25$], while the converse was found in another female [378 total, $P(\chi^2 \geq 5.42) > 0.05$]. These differences probably reflect individual variation since the majority of specimens had nearly equal numbers of oocytes between ovaries, and there was no consistent pattern in those with a significantly skewed distribution of oocytes.

The total number of mature oocytes in a female was positively correlated with increasing SL and adjusted body weight. For 12 gravid females the regression of number of mature oocytes (F) on SL was $F = -321.6 + 5.9$ SL ($r = 0.68$), and

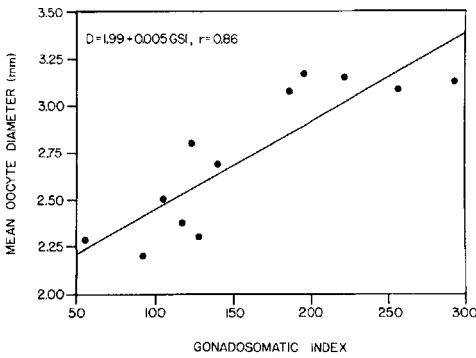


FIGURE 4. Relationship between mean vitellogenic oocyte diameter and GSI of mature female *N. flavus*.

number of mature oocytes on adjusted body weight in grams (W) was $F = 152.0 + 9.1W$ ($r = 0.70$; fig. 5). The number of mature oocytes per gram adjusted body weight ranged from 13.3 to 19.0 ($\bar{x} = 15.5$; $N = 12$).

SEX RATIO. There was no significant deviation from a 1:1 sex ratio in the total sample from the Vermilion River (114 females: 113 males), nor in any of the monthly samples from the summer. Accounts of skewed sex ratios in other species of *Noturus*, particularly in older age classes, were reviewed previously (Mayden and Burr 1981) and were thought to have resulted from sampling bias in at least some of the studies cited.

NESTING. As with other species in the genus, *N. flavus* spawns from early to mid-summer when water temperature exceeds about 25°C (table 1). Nests were found beneath very large rocks (mean dimensions 43 × 28 × 13 cm) in water 53-117 cm ($\bar{x} = 87$ cm) deep. In the Meramec River, nests were found in areas of moderate current and slightly turbid water; nest rocks were covered with filamentous algae and partially imbedded in loose gravel. In the Vermilion River a single clutch of embryos was found beneath a large flat rock in a strong riffle in very turbid water.

Nests were guarded by single adult males ranging in size from 87 to 105 mm

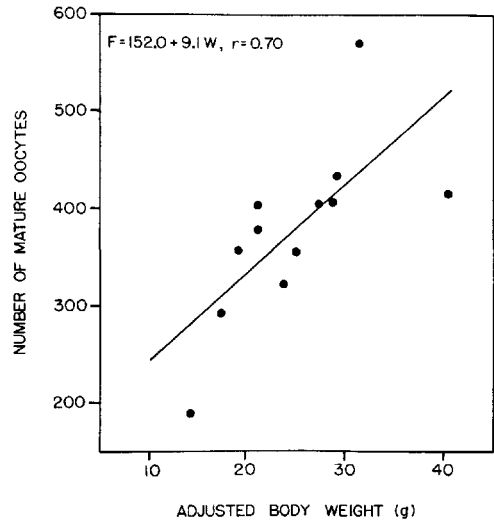


FIGURE 5. Relationship between number of vitellogenic oocytes and adjusted body weight of mature female *N. flavus*.

($\bar{x} = 94.8$ mm). Four of the nests contained complete broods of adherent embryos ranging in number from 104 to 208 ($\bar{x} = 174$) and in age from about 24 h to immediately pre-hatching. Three additional clutches contained larvae in various stages of development (five-nine d post-hatching) and were guarded by adult males. Larvae were negatively phototactic and dispersed rapidly when nest cover was removed or were dispersed by the current, precluding capture of complete broods. One such brood had at least 306 meta-larvae, the largest number of young captured in any nest. Pre-hatchling embryos were 2.6-4.0 mm ($\bar{x} = 3.4$ mm; $N = 40$) in diameter, which is near to the size (3.5-4.0 mm) reported by Greeley (1929).

LARVAL DEVELOPMENT. Chorion diameters of 30 pre-hatchling embryos (10-15 h) ranged from 2.6 to 4.0 mm ($\bar{x} = 3.4$ mm). Yolk sacs of developing embryos were whitish to light yellow, compared with darker yellow or nearly orange yolks in *N. albatel* (Mayden et al. 1980), *N. exilis* (Mayden and Burr 1981), *N. miurus* (Burr and Mayden 1982a), and

N. nocturnus (Burr and Mayden 1982b). Yolk diameters averaged 3.3 mm (range = 3.0-3.6 mm; N = 20). Eight embryos at 10 h had ventrally flattened yolk sacs, resulting in a space about one mm between the chorion membrane and yolk surface.

Early morphogenesis and chronology of pre-hatchling life-history could not be determined due to high mortality of embryos in the laboratory. Specimens reared at 25°C (obtained from a single clutch of 104 immediately prior to hatching) were preserved at various intervals to observe post-hatching development.

At hatching, mesolarvae ranged in TL from 6.7 to 7.5 mm (\bar{x} = 7.0; N = 5), had well-developed maxillary and mandibular barbels, rudimentary or no nasal barbels, darkly pigmented retinæ, small pectoral fin buds, and had a continuous posterior fin fold heightened in the regions of the anal and dorsal fins and with rudimentary caudal fin rays. Head lengths of early mesolarvae (<2 d; N = 5) averaged 22% of TL, and maximum head depths averaged 22% of TL. Young thus appeared somewhat more robust than mesolarvae of other species (Mayden et al. 1980, Mayden and Burr 1981, Burr and Mayden 1982a, b). Hatchlings of *N. flavus* exhibited tightly cohesive schooling behavior.

At two d post-hatching, mesolarvae ranged in TL from 7.5 to 8.6 mm (\bar{x} = 8.2 mm; N = 3), had small melanophores scattered over the dorsal surface of the head and trunk, small pelvic fin buds, and rudimentary rays differentiated in all of the remaining fins.

Increased growth, yolk absorption, pigmentation, and fin differentiation characterized development during the first week following hatching. Two four-d-old specimens averaged 10.0 mm TL. By seven d post-hatching (fig. 6a), yolk absorption was nearly complete and specimens were moderately pigmented on the dorsum, especially on the head, and averaged 12.6 mm TL (range = 12.2-13.0 mm;

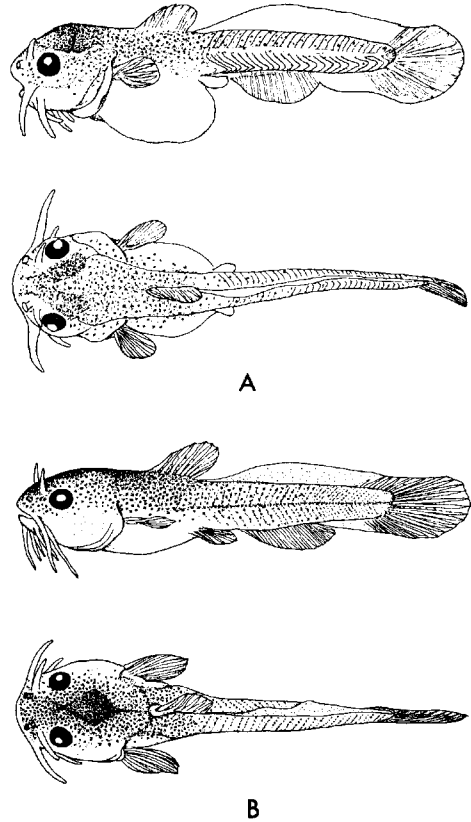


FIGURE 6. Late larval development of *N. flavus*. A) Lateral and dorsal view of seven-d metalarva (12.9 mm TL) and B) lateral and dorsal view of juvenile (17.8 mm TL) from Meramec River, Missouri.

N = 4). At 10 d metalarvae averaged 13.1 mm TL (range = 12.5-13.4 mm; N = 11), had completely resorbed their yolk sacs, and were uniformly pigmented on the sides and dorsum similar to adults. Head lengths averaged 25% and head depths 17% of TL in five 10-d-old metalarvae, approximating proportions given for 20-21 mm specimens (Fish 1932, Tin 1982). At 12 days (mean TL = 13.3 mm; N = 17) and beyond, late metalarvae and juveniles (fig. 6b) resembled adults in body proportions and pigmentation.

DIET. Specimens from the Vermilion River were taken from May to September, precluding an analysis of seasonal changes in the diet. However, there were some differences between different-sized individuals in the food organisms they consumed during the summer months (table 2). Specimens from 60-100 mm had the greatest diversity of food organisms. Mayfly naiads were consumed by *N. flavus* at all sizes, and stonefly, caddisfly, and midge larvae were found in stomach contents of specimens of all sizes except those greater than 120 mm. Black fly larvae were only found in specimens less than 80 mm. Conversely, crayfish were not eaten by fish smaller than 60 mm but were found in a high percentage of stomachs of specimens

over 80 mm and were the bulkiest food items. The percentage of stomachs containing caddisfly and midge larvae tended to decrease with increasing fish size, whereas the occurrence of mayfly naiads remained relatively high in all size classes. The remaining invertebrates, unidentified teleost eggs, and remains of the fantail darter, *Etheostoma flabellare*, were infrequently present in the diet. Attesting to the diversity of organisms consumed, one specimen from the Mississippi River drainage had the following items in its stomach: 10 ephemeropteran larvae, two trichopteran larvae, nine dipteran pupae (one tipulid, eight chironomids), one dipteran larva (a simuliid), one annelid, one amphipod, and one chilopod.

TABLE 2

Stomach contents of N. flavus from Vermilion River drainage, Illinois, by 20-mm-size classes. Figures above are percentages of stomachs containing food organisms; parenthetical figures beneath are mean numbers of food organisms per stomach.

Food Organism	Size Class					
	≤40 mm (N = 5)	41-60 mm (N = 11)	61-80 mm (N = 15)	81-100 mm (N = 11)	101-120 mm (N = 9)	>120 mm (N = 3)
Nematoda	—	—	6.7 (2.0)	9.1 (1.0)	—	—
Crustacea	—	—	6.7 (1.0)	36.4 (1.0)	33.3 (1.0)	33.3 (1.0)
Insecta						
Plecoptera	20.0 (1.0)	18.2 (2.5)	46.7 (1.4)	9.1 (2.0)	22.2 (2.0)	—
Ephemeroptera	80.0 (2.0)	54.5 (1.7)	73.3 (3.2)	36.4 (3.7)	77.8 (3.6)	66.7 (3.0)
Odonata (Zygoptera)	—	—	6.7 (1.0)	9.1 (2.0)	—	—
Megaloptera	—	—	6.7 (1.0)	9.1 (1.0)	11.1 (1.0)	—
Trichoptera	100.0 (2.6)	90.9 (14.8)	46.7 (4.6)	27.3 (1.3)	22.2 (1.5)	—
Coleoptera	—	—	6.7 (1.0)	—	—	—
Diptera						
Simuliidae	20.0 (1.0)	18.2 (3.0)	6.7 (1.0)	—	—	—
Chironomidae	40.0 (1.0)	18.2 (2.0)	40.0 (2.3)	9.1 (2.0)	11.1 (1.0)	—
Teleostei						
Eggs	—	—	6.7 (1.0)	—	—	—
<i>Etheostoma flabellare</i>	—	9.1 (1.0)	—	—	—	—

Despite the close proximity to sites where specimens were taken for this study, *N. flavus* in Jordan Creek, Vermilion Co., Illinois, differed from our samples in that they fed heavily on isopods and amphipods during certain times of the year (Angermeier 1982). It is possible that our sample size was too small or seasonally-limited to detect maximum prey diversity or that there may be a significant difference in benthic invertebrate faunas between Jordan Creek and the Middle and Salt Forks of the Vermilion drainage.

PARASITES. Of 60 specimens examined for endoparasites of the digestive tract, liver, and coelom, 83.3% showed no evidence of parasitism and 13.3% had adult trematodes (*Crepidostomum* sp.) ranging in number from one to 17 ($\bar{x} = 4.3$) per fish lodged in the intestinal epithelium or free within the lumen. Adults of the acanthocephalan, *Leptorhynchoides thecatus*, were found within the intestines ($\bar{x} = 7$ parasites per fish) or encysted in the coelom ($\bar{x} = 5$ parasites per fish) in 3.3% of fish examined. Unidentified nematodes found in the stomachs of two specimens were assumed to have been ingested as free-living forms. Hoffman (1967) listed a total of four species of trematodes, two cestodes, one nematode, and two acanthocephalan parasites previously reported from *N. flavus*.

DISCUSSION

The general biology of *N. flavus* as outlined here is similar to that in previous reports. There are, however, a few differences between Great Lakes populations and those from more southern inland streams. These relate to maximum body length, longevity, absolute fecundity (number of mature oocytes per year), and possibly diet. Both Gilbert (1953) and Trautman (1981) found that individuals along shore regions of western Lake Erie attained much greater lengths (2.0-2.5 \times), weights (3.0 \times), and ages than those from southern inland streams of Ohio. Stream individuals generally did not live more than six yr (10 six-yr-old specimens averaged

126 mm SL), but Lake Erie samples included 14 specimens ($\bar{x} = 209$ mm SL) in their seventh year and one (233 mm SL) in its ninth year (Gilbert 1953). Individuals of 305 mm TL (about 258 mm SL) and 312 mm TL (about 264 mm SL) were recorded by Scott and Crossman (1973) and Trautman (1981), respectively, from Lake Erie. Our data on ages and lengths of adults from Illinois and Missouri streams and those data of specimens collected from a South Dakota stream (Carlson 1966) corroborate the findings of Gilbert (1953) and Trautman (1981) that individuals of *N. flavus* in streams rarely live over six yr and rarely exceed 180 mm SL.

There may also be differences in absolute fecundity between individuals of lake and stream populations of *N. flavus*. Langlois (1954) gave a mean of 973 (range = 767-1205) apparently-mature oocytes in females from Lake Erie without indicating sample size and lengths of females examined; his mean was greater than 2.5 times the mean number (377.8) of mature oocytes reported here. An estimated clutch size of 500 in one nest from Sister Creek (Lake Erie drainage), New York (Greeley 1929) was over twice the mean number of spawned eggs found in Illinois and Missouri nests. The large body size attained by individuals in Lake Erie probably accounts for differences in absolute fecundity and number of spawned eggs between females of lake and stream populations of *N. flavus*, since absolute fecundity is positively correlated with body length.

Noturus flavus feeds on a wide variety of benthic organisms, primarily aquatic larval insects, decapod crustaceans, molluscs, and other fishes and their eggs. While there may be some geographic differences in diet between individuals from Lake Erie (Greeley 1929, Bowman 1936, Gilbert 1953, Langlois 1954, Wolfert et al. 1975) and those from inland streams (Cahn 1927, Pflieger 1975, Angermeier 1982, this study), additional studies are needed before meaningful comparisons can be made on seasonality of diet, feeding periodicity, and foods consumed at different sizes.

Presently, individuals of *N. flavus* may be considered benthic, opportunistic, and probably nocturnal (Bowman 1936) feeders that may consume larger prey as their own body lengths increase.

There are no known differences in spawning period, nesting sites, spawning temperatures, and size of embryos and larvae (Greeley 1929, 1934, Langlois 1954, Fish 1932, Tin 1982) between Great Lakes and stream populations of *N. flavus*. There are distinct color differences between individuals from the two populations (Trautman 1981) and additional studies, perhaps including isozyme analyses, might prove useful in determining if these populations of *N. flavus* are subspecifically distinct.

Relative to its congeners, the life-history of *N. flavus* represents one extreme of a continuum. Present knowledge of species of *Noturus* is inadequate to be certain about factors which have molded life-history patterns of the genus. Nonetheless, there are enough data from studies of more than half of the species to recognize putative rank of reproductive potential of each relative to its congeners (Mayden and Walsh 1984); the gradation of maximum body lengths from a minimum of about 36 mm SL in *N. stanauli* (Etnier and Jenkins 1980) to greater than 250 mm SL in *N. flavus* is paralleled by some overlap of life-history traits among species. From what is known of the 25 described matoms, *N. flavus* is the largest, lives the longest, matures later in life (3-4 yr) and at a longer SL than others, and has the greatest absolute fecundity. This combination of characteristics has not been found in any congener, although some species have individual traits that approach those of *N. flavus*.

Mean annual absolute fecundity of *Noturus* ranges from 24 and 30 oocytes per female in *N. leptacanthus* and *N. hildebrandi*, respectively (Mayden and Walsh 1984), to 378 in *N. flavus* (this study). The next-to-greatest absolute fecundity (\bar{x} = 240 oocytes) is that of *N. flavater*,

the second-largest species (nine females averaged 92.8 mm SL; Burr and Mayden 1984). Absolute fecundities of other species overlap somewhat within the above range (Mayden and Walsh 1984), but as expected there is a positive correlation between increasing body size and greater fecundity in the genus.

Because of inter- and intraspecific variation in GSI, relative fecundities (ratio of number of oocytes per unit body weight) are more valuable in comparisons of reproductive potentials. Based on predicted mature body weights (converted from lengths), Clark (1978) estimated relative fecundities for 13 ictalurids as ranging from 0.6 (*Ictalurus melas*) to 18.5 (*N. leptacanthus*) oocytes g^{-1} body weight, and estimated a mature body weight of 160 g and a fecundity of 2.2 oocytes g^{-1} body weight for *N. flavus*. However, most individuals of *N. flavus*, except perhaps those in Lake Erie, mature at much smaller weights and very large females would have proportionally greater fecundities. Females of *N. flavus* in this study had a mean relative fecundity of 15.5 oocytes g^{-1} body weight; relative fecundity of other species of *Noturus* ranges from about 10 to 40 oocytes g^{-1} body weight (Mayden and Walsh 1984). Hence, *N. flavus* is more fecund than congeners in number of progeny per female, but mature females are larger and produce slightly fewer oocytes per gram body weight than most species of the genus that have been studied.

There is circumstantial evidence that some females of some species may spawn with more than one male in a breeding season (Menzel and Raney 1973, Clark 1978, Mayden and Burr 1981). In this study, the mean number of vitellogenic oocytes (377.8) was greater than twice the mean number of embryos (174.5) from complete broods of *N. flavus*. However, polyandry could not be affirmed from broods guarded only by males, due to the positive correlation between female body size and clutch size and to the lack of direct observations of spawning or capture of par-

tially spent females accompanying nesting males.

The combination of life-history characteristics of *N. flavus* is at one extreme in the genus, as a consequence of the species' large size and greater longevity relative to congeners. Maternal investment in reproductive effort per season of *N. flavus*, in terms of number and size of offspring, is lower than other species of *Noturus* as a result of the trade-off for increased somatic growth. Female *N. flavus*, however, mature later but live longer than the other species, have larger clutches with increasing body size and age, and presumably produce more broods during their lives.

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