

## Effects of Photoperiod on Behavior and Courtship of the Neosho madtom (*Noturus placidus*)

Angela G. Bulger<sup>a</sup>  
 Department of Biological Sciences  
 Emporia State University  
 Emporia, KS 66801 USA

Mark Wildhaber  
 Columbia Environmental and Contaminants Research Center  
 USGS, BRD  
 Columbia, MO 65201 USA

and

David Edds  
 Department of Biological Sciences  
 Emporia State University  
 Emporia, KS 66801 USA

### ABSTRACT

To test effects of long and short day-length on behavior of the Neosho madtom (*Noturus placidus*), we held six pairs of fish in separate tanks under 16 hr (L): 8 hr (D) (long-day) and six pairs under 12 hr (L): 12 hr (D) (short-day) photoperiods. An ethogram was created and behavior was electronically and continuously recorded. Two-minute intervals for each hour over four 4-day periods were examined, and proportion of time active and performing specific behaviors in each tank was analyzed to compare differences between treatments. Individuals held under 16 L, 8 D were more active during the light cycle than those in 12 L, 12 D. Specific behaviors examined included resting, swimming, feeding, aggression, cavity enhancement, and courtship. A higher proportion of time was spent performing cavity enhancement, cavities were deeper, and gravel size in cavities was smaller for those fish in the long-day treatment. Throughout the experiment various courtship behaviors were observed in male-female pairs held in 16 L, 8 D, but no such behaviors were observed in 12 L, 12 D. The relationships between a long photoperiod and activity, cavity enhancement, and courtship behaviors illustrate the influence of photoperiod on the Neosho madtom reproductive cycle.

### INTRODUCTION

Little is known about the behavior of diminutive stream fishes (Matthews 1998), especially the madtoms, a group of small, nocturnal North American catfishes of the genus *Noturus*. Information regarding the effects of photoperiod on activity and behavior is lacking in this group, especially with regard to spawning. The Neosho madtom, *Noturus placidus*, is listed as threatened by the U.S. Fish and Wildlife Service (USFWS). The USFWS (1991) Neosho madtom recovery plan regarded understanding the reproductive biology and behavior as critical for recovery of this species.

Due to high river turbidity and flow, behavioral observations in the field are nearly impossible during the presumed spawning season (late May through early July), thus no Neosho madtom spawning or nests have been observed in the wild (Pfungsten and Edds 1994). Attempts at captive propagation have had limited

<sup>a</sup>Present address: 14801 W. 149th Ct., Olathe, KS 66062 USA

success. Of four clutches laid in captivity, one did not develop and was likely never fertilized (Pfungsten and Edds 1994), one resulted in 43 surviving fish (Wilkinson and Edds 1997), one was presumably consumed by the spawning male (Bulger 1999), and one resulted in two surviving Neosho madtoms (Bulger 1999).

Understanding environmental cues that trigger spawning could increase success of captive propagation, which is essential for studying *N. placidus* breeding biology and behavior, and could be necessary for successful reintroduction efforts. Photoperiod is one important factor in stimulating sexual maturation and ovulation in many fishes (Wootton 1990), including madtoms (Dinkins and Shute 1996), and may play an important role in triggering captive spawning. In addition, there is need to understand how manipulating photoperiod affects other behaviors important to the fish in captivity. For example, effects of increased photoperiod on feeding and aggression need investigation, as well as influences on overall activity levels.

Our research focused on the effects of a long and short photoperiod on behavior of the Neosho madtom. Objectives were to investigate the influence of photoperiod on captive propagation by examining activity and the following specific behaviors: resting, swimming, feeding, aggression, cavity enhancement, and courtship.

## METHODS AND MATERIALS

Fish were collected from the Cottonwood River, Chase and Lyon counties, Kansas, and transported to the Columbia Environmental Research Center (CERC) in Columbia, Missouri. Eight individuals were captured on 13 August 1996 and 21 individuals were collected on 17 and 18 May 1997. Fish were kept in four 59-l holding tanks at 18 to 21°C under a 13.5 hr (L): 10.5 hr (D) photoperiod.

We placed twelve 29.5-l aquaria in an isolation chamber which was divided with black plastic to create two treatment conditions, with regard to photoperiod. Well water (pH = 7.5) in each tank was maintained at 20 cm depth and 25 - 27°C. Water was delivered continuously with a turnover rate of approximately 8.6 l h<sup>-1</sup>. The bottom of each tank was covered approximately 4 cm deep with 2 to 24 mm diameter gravel. Structure was provided by cutting 12.5-cm PVC pipes in half lengthwise, which resulted in a U-shaped shelter; the PVC provided cover while allowing observation from the front of the tank. Light was provided by fluorescent bulbs mounted in the chamber. Fish were fed a diet of live amphipods (*Hyalella azteca*) and blackworms (*Lumbriculus* sp.) every two to three days in both treatment aquaria and holding tanks.

On 28 May 1997, we placed two fish into each of six experimental tanks at 18 to 21°C and 13.5 L: 10.5 D photoperiod. Attempts were made to determine sex of each individual based on secondary sex characteristics (Pfungsten and Edds 1994) so that each tank would contain one male and one female. Individuals not placed in study tanks remained in holding tanks. Over the next three weeks we acclimated all fish (treatment and holding tanks alike) to the experimental temperature of 25°C. From 12 to 14 June, while water temperature was 21°C, we collected baseline behavior and activity data on all fish in the treatment chamber.

On 16 June, we adjusted day-length to treatment settings of 16 hr (L): 8 hr (D), the long-day treatment, or 12 hr (L): 12 hr (D), the short-day treatment. On 23 June, we removed five individuals due to health problems or lack of development of secondary sexual characteristics, and replaced them with

individuals from the holding tanks. After a five-day acclimation period, the first experimental period began 28 June. On 9 July, we replaced nine fish with individuals from the holding tanks. After a five-day acclimation period, a second experimental period began 14 July.

Three Panasonic closed circuit black and white TV cameras were mounted on each side of the isolation chamber so that each camera recorded activity in two tanks. Infrared illuminators were mounted above the tanks to allow recording of nighttime behaviors. A real-time and time-lapse VCR was used to record Neosho madtom behavior 24 hr per day.

In addition to recording the control activity (12 to 14 June), we filmed behavior continuously during four 4-day periods, which comprised two experimental periods (first experimental period: 28 June - 1 July; 4 July - 7 July; second experimental period: 14 July - 17 July; 20 July - 23 July), simultaneously for both long- and short-day treatments. We then analyzed 2 min, selected randomly, of each hour for each tank during the control and experimental periods; observations were not made during feeding or tank maintenance. Each time the behavior of an individual changed during the 2-min interval, we recorded the time and new behavior. Attempts were made to record the behaviors of each individual separately, but due to poor film quality and the small size of the fish this was not always possible; however, this collection method allowed us to determine the time spent performing each behavior in each tank. Behaviors recorded (Table 1) were taken from an ethogram created from a combination of observations of Neosho madtoms by A. Bulger, observations made during previous attempts at Neosho madtom captive breeding (Pfungsten and Edds 1994, Wilkinson and Edds 1997), and from descriptions of spawning behavior of the brown madtom (*Noturus phaeus*; Chan 1995). Following completion of the study, we euthanized all fish and examined them internally to verify sex.

We classified each behavior as either active or inactive (resting). The proportion of time spent active in each tank in control groups was compared by using a Wilcoxon-Mann-Whitney two-tailed test of ranks with the null hypothesis that there was no difference in activity between the two treatments ( $\alpha=0.05$  for all analyses). The proportion of time spent active in light versus dark hours was also tested in each treatment group by using a Wilcoxon-Mann-Whitney one-tailed test under the alternative hypothesis that activity of this nocturnal fish was higher during the dark than during the light cycle of the photoperiod. A Wilcoxon-Mann-Whitney two-tailed test was also performed on the proportion of time spent active in each tank with the null hypothesis that activity did not differ between the two experimental periods.

To assess effects of photoperiod on behavior, we assigned each behavior from the ethogram one of six specific behavior types: resting, swimming, feeding, aggression, cavity enhancement, and courtship (Table 1); resting behaviors were not included in analysis, as they are the complement of active behavior. We compared the proportion of time spent performing each behavior type in light and dark hours between treatment groups for both experimental periods by using a Wilcoxon-Mann-Whitney two-tailed test.

To examine effects of photoperiod on cavity enhancement for nesting, we measured depth of the gravel substrate under and outside the structure at the end of the study. We also measured the diameters of three randomly chosen pieces of gravel from under the structure, and three from the rest of the tank. These

Table 1. Ethogram of Neosho madtom Behaviors performed by either or both fish during experimental periods. Each behavior is labeled as I = inactive or A = active (resting), and categorized as a behavior type: resting, swimming, feeding, cavity enhancement (cav enhan), aggression, and courtship.

Behavior	Description	Activity	Type
<i>Performed by either fish:</i>			
Upside down	resting upside down under structure	I	resting
Quiet in	resting quietly under structure	I	resting
Quiet out	resting quietly out of structure	I	resting
Restless in	moving slightly about under structure	I	resting
Restless out	moving slightly about outside of structure	I	resting
Circle alone	swimming in circles against glass at front, back, or side of tank	A	swimming
Swim	swimming in no particular pattern	A	swimming
Feeding	feeding	A	feeding
Headstand	vertical in water nudging rocks with head	A	cav enhan
Rock move	moving a rock in its mouth (picks up rock and drops it in another place)	A	cav enhan
Spin	swimming in circular pattern under structure	A	cav enhan
Fanning	fanning tail while resting under structure	A	courtship
<i>Performed by both fish:</i>			
Quiet in both	both fish resting quietly under structure	I	resting
Quiet out both	both fish resting quietly out of structure	I	resting
Restless in both	both fish slightly moving about under structure	I	resting
Restless out both	both fish slightly moving about out of structure	I	resting
Circle chase	one fish chases other in circular pattern in front, back, or side of tank. Individuals periodically meet and have some sort of physical contact (rub, bite, or nudge)	A	swimming
Bite	one fish bites at body of other fish	A	aggression
Chase	one fish chases other in no particular pattern	A	aggression
Nudge	one fish nudges resting individual and swims away or rests next to it. Nudged individual may swim or remain resting	A	aggression
Jostle	fish switch positions back and forth under structure between short periods of rest	A	courtship
Carousel	fish swim together head to tail in small circular pattern under structure	A	courtship
Tail Curl	fish lay side by side, head to tail; male tail wrapped around head of female and both fish quiver. This behavior was only seen following carousel	A	courtship

measurements allowed us to compare the depth of the cavity and gravel size within the cavity in each tank, compared to the rest of the tank bottom, and to compare cavity depth and gravel size between treatments by performing Wilcoxon-Mann-Whitney two-tailed tests. A Pearson correlation coefficient was calculated to examine strength of the relationship between cavity depth and gravel size within the cavity.

**RESULTS**

Throughout the control and treatment periods, 36 pairs of Neosho madtoms was observed in the isolation chamber. Subsequent internal examination allowed sexing of 23 pairs and revealed 12 as male/female, 10 as female/female, and one as male/male; sex of one or more individuals in other pairs was equivocal (Table 2). Each treatment group had two male/female pairs during each data collection period. In addition, during the first experimental period, camera failure caused uneven sample sizes; two short-day tanks were not continuously monitored.

Table 2. Sex of Neosho madtoms in study tanks during study periods (M=male, F=female, U=undetermined), with depth of cavity (mm) under structure (depth of gravel outside structure - depth of gravel under structure) and difference between mean diameter (mm) of gravel outside structure and under structure at end of experiment.

	Tank	Control Period	Experimental Period 1	Experimental Period 2	Cavity Depth	Gravel Size Difference
long-day	1	M/F	M/F	M/F	15	4.3
	2	F/F	F/F	F/F	37	7.3
	3	F/F	F/F	F/F	25	2.3
	4	M/F	M/F	M/F	33	4.4
	5	U/U	U/U	U/F	11	4.0
	6	U/U	U/F	F/F	22	5.0
short-day	7	M/F	M/F	M/F	5	2.3
	8	M/U	M/U	M/U	4	-3.7
	9	U/U	U	M/M	1	-2.0
	10	M/F	U/F	M/F	16	1.0
	11	U/F	U/F	F/F	3	7.7
	12	F/F	M/F	F/F	11	1.5

Results from the control period, 13.5 hr (L): 10.5 hr (D), showed no significant difference between groups in the proportion of time spent active in the dark or light (Mann-Whitney U:  $Z=-0.88$ ,  $P=0.38$  and  $Z=-0.61$ ,  $P=0.54$ , respectively). We performed analyses on each experimental period separately for three reasons. First, the Wilcoxon-Mann-Whitney test showed a significant difference in the proportion of time spent active by individuals in the short-day treatment; more activity was seen during the second experimental period than during the first in the dark cycle of the photoperiod ( $Z=-2.24$ ,  $P=0.03$ ). Second, the sample sizes were uneven because of a camera failure during the first experimental period. Third, individuals in both short- and long-day treatment

groups had been moved or replaced, thus the test subjects were different. Additionally, based on what is known of the life history of the Neosho madtom, the fish has a short spawning period, mainly during June and July (Bulger and Edds, 2001). The time lag between 28 June and 14 July might impact spawning behavior.

Neosho madtoms spent a significantly higher proportion of time active during dark hours versus light hours (long-day: first experimental period  $Z=2.80$ ,  $P=0.005$ ; second experimental period  $Z=2.80$ ,  $P=0.005$ ; short-day: first experimental period  $Z=2.17$ ,  $P=0.03$ ; second experimental period  $Z=2.80$ ,  $P=0.005$ , Fig. 1). Comparison of the proportion of time spent active during the second experimental period showed individuals in long-day treatment were more

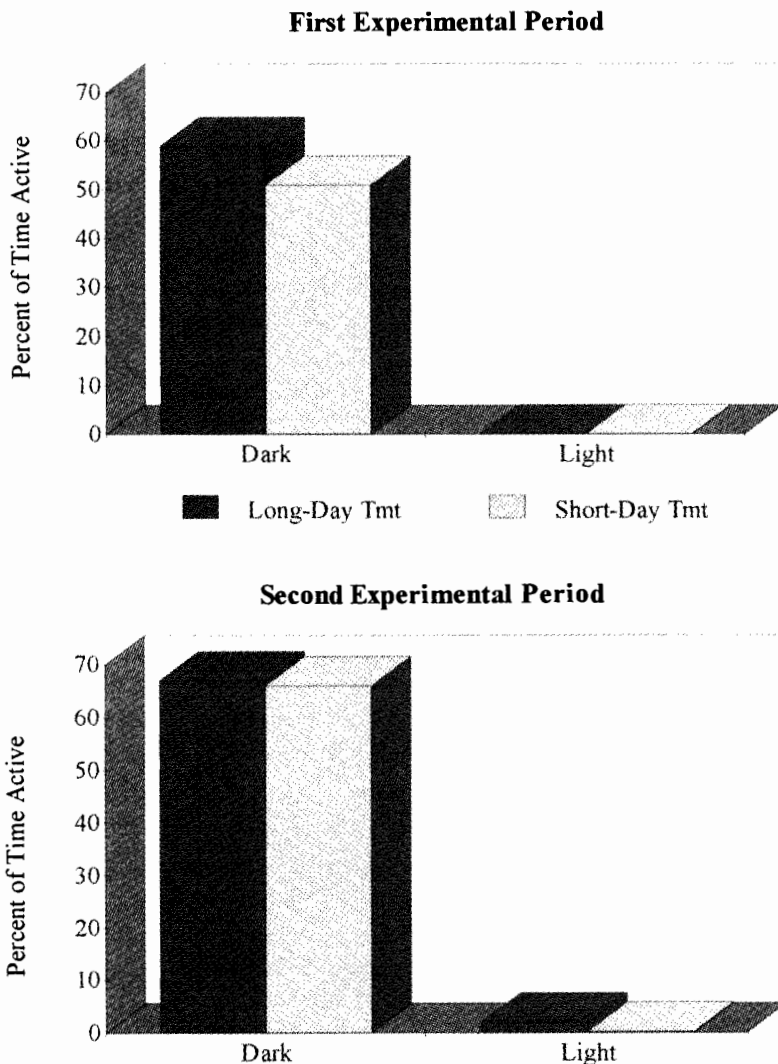


Figure 1. Percent of time active in dark and light of each treatment (short-day and long-day) during the first and second experimental periods.

active during the light cycle than those in short-day treatment ( $Z=2.00$ ,  $P=0.05$ , Fig. 1). We observed individuals in long-day treatment swimming about or foraging for food 1 to 2 h before the light cycle ended. This difference in activity was not statistically significant during the first experimental period ( $Z=-1.81$ ,  $P=0.07$ ). During dark hours, there was no significant difference in activity levels (first experimental period  $Z=-0.96$ ,  $P=0.34$ ; second experimental period  $Z=0.40$ ,  $P=0.58$ , Fig. 1).

We compared the proportion of time spent performing the following behaviors between the two treatment groups in dark and light hours for each collection period: swimming, feeding, aggression, and cavity enhancement. The proportion of time spent swimming, feeding, and performing aggressive behaviors was not different between treatments. During the second experimental period, individuals held under the long-day photoperiod spent a higher proportion of time performing cavity enhancement in dark hours than those in the short-day photoperiod ( $Z=2.00$ ,  $P=0.05$ ). Although not significant in the first experimental period or in light, the proportion was consistently higher in long-day treatment. Specific cavity enhancement behaviors included the "spin," in which one individual would spin in circles just above the gravel under the structure; the "headstand," in which one individual would hover at approximately  $45^\circ$  and nudge rocks from under the structure by using its head; and the "rock move," in which gravel was carried in the mouth from under the structure and dropped outside. Both males and females were observed performing the spin and the headstand, but only males were observed doing the rock move.

No spawning was observed during this study; however, based on observations of other madtom species (Bowen 1980, Fitzpatrick 1981, Chan 1995), and observations during previous Neosho madtom breeding studies (Pfungsten and Edds 1994, Wilkinson and Edds 1997), behaviors were seen in this study that indicated courtship (Bulger 1999). No statistical analyses were performed on courtship behaviors because of small sample size. However, throughout the course of the study male/female pairs held in long-day photoperiod were observed performing courtship behaviors (Table 1), including the "carousel" (88 times), the "tail curl" (36 times), the "jostle" (four times), and the "fan" (once); these behaviors were never observed in male/female pairs held under short-day conditions.

Depressions under structures indicated cavity enhancement. Cavity depth ranged from 1 to 37 mm (Table 2). Cavities deeper than 20 mm were made in four of 12 tanks; all four were in long-day treatment. In addition, the deepest cavity was constructed by females in a long-day treatment. In long-day treatment, cavities were deeper ( $Z=-2.32$ ,  $P=0.02$ ) and gravel size within cavities were smaller ( $Z=1.79$ ,  $P=0.02$ ) than in short-day treatment. Mean gravel diameters within cavities in long-day treatment ranged from 12.0 mm to 16.7 mm ( $\bar{x}=14.5$ ,  $SD=3.42$ ); in short-day treatment means ranged from 14.0 mm to 23.7 mm ( $\bar{x}=18.1$ ,  $SD=4.84$ ). Pearson's correlation coefficient between gravel size and cavity depth suggested a negative relationship ( $r=-0.55$ ), but was not significant ( $P=0.07$ ).

## DISCUSSION

Results indicated higher activity in the dark than during the light cycle, as expected for a nocturnal fish. Higher activity levels during the light cycle in the second experimental period in long-day treatment could be attributed to restlessness; individuals were more active just prior to the onset of the dark cycle. Reasons for differences in activity between the early and late experimental periods are unknown. No breeding behaviors and very few cavity enhancement behaviors were seen during the light cycle; most activity was swimming behavior. Perhaps the five-day acclimation period was not long enough for fish to experience photoperiod effects.

Analysis of swimming, feeding, and aggression indicated no significant differences between the two treatment groups, which suggests that photoperiod does not play a role in these behaviors. Madtoms may limit or refrain from feeding during spawning season, especially males caring for eggs or larvae (Clark, 1978, Mayden and Burr 1981, Burr and Mayden 1982, Dinkins and Shute 1996).

Cavity enhancement behaviors were considered important because it is well documented that other madtom species use nests during spawning. During the second experimental period individuals held in long-day treatment spent a higher proportion of time performing cavity enhancement behaviors in the dark than fish in short-day treatment and, although differences were not significant, the proportion was consistently higher in long-day treatment throughout the study. A difference was also seen in cavity depth and gravel size within cavities in tanks in long-day treatment at the end of the study. These individuals probably put more effort into cavity enhancement; however, cavity measurements were taken only at the completion of the study, and because cavity enhancement was apparent in both sides of the treatment chamber within the first two weeks of the study, possibly individuals held in short simulated daylight hours reduced the amount of energy they put into cavity enhancement in response to reduced day-length (13.5 L, 10.5 D in holding tanks, 12 L, 12 D in treatment tanks). No photoperiod effect was seen in the proportion of time spent performing cavity enhancement during the first experimental period, but a significant difference was seen between treatments during dark hours in the second experimental period. This suggested that keeping Neosho madtoms in short-day photoperiod with 25 to 27°C water temperatures over a one-month period was not sufficient to encourage cavity enhancement behaviors.

Cavities were enhanced in tanks containing both male/female and female/female pairs. Most cavity enhancement behaviors observed were performed by males; however, females were observed performing the headstand and the spin, in tanks containing only females, which suggested that females also play a role in cavity enhancement. Wilkinson and Edds (1997) also observed both male and female Neosho madtoms nudging rocks out of cavities to create depressions in the substrate. Female brown madtoms initiated nest construction and aided nest maintenance before breeding (Chan 1995), and both male and female freckled madtoms participated in nest construction prior to spawning (Fitzpatrick 1981), but Mayden and Burr (1981) reported that males were solely responsible for nest construction in the slender madtom. In most other *Noturus* species it is unknown whether nest construction is performed by males, females, or both. Cochran (1996) also observed stonecats (*N. flavus*), tadpole madtoms (*N. gyrinus*), and a black madtom (*N. funebris*) enlarging cavities by moving rocks in



their mouths, and Fitzpatrick (1981) observed a male brindled madtom remove gravel from a can by taking rocks into his mouth and dropping them outside the can opening. No other accounts of behaviors used to enhance cavities have been reported for *Noturus* species; however, brown bullheads (*Amieurus nebulosus*) and flathead catfish (*Pylodictis olivaris*) have been observed moving rocks in their mouths for nest construction (Breder and Rosen 1966).

The male/female pairs held in long-day treatment performed courtship behaviors, including the carousel, tail curl, jostle, and fan, but those held in short-day conditions did not perform such behaviors. Östlund and Ahnesjö (1998) reported that male courtship displays, such as fanning and body shakes, influenced female mate choice and hatching success in fifteen-spined sticklebacks (*Spinachia spinachia*). Thus, the increase of such courtship displays by individuals held in long-day treatment could indicate the importance of photoperiod in stimulating such behavior.

Sundararaj and Sehgal (1970) found a long photoperiod to be important in stimulating the ovarian cycle of a seasonally breeding catfish, *Heteropneustes fossilis*, which is native to areas where seasonal day length varies by only 4 h. Likewise, de Vlaming (1972) reported photoperiod to be a major environmental cue triggering reproductive cycles of salmonids and gasterosteids. The importance of photoperiod to stimulating the breeding cycle is most likely related to the benefits of timing the spawn to coincide with juvenile food availability, which may optimize survival of offspring (Jobling 1995).

Our study provided the first ethogram and quantitative observations of the effects of photoperiod on Neosho madtom behavior including resting, swimming, feeding, aggression, cavity enhancement, and courtship. The proportion of time spent performing cavity enhancement behaviors was higher in fish held under the long photoperiod, and more courtship behaviors were observed in those individuals. Results of this study were consistent with the hypothesis that photoperiod plays a role in the breeding cycle of this fish.

#### ACKNOWLEDGMENTS

We sincerely thank the many people who assisted with this study, including: A. Allert, C. Annett, M. Annett, V. Annett, J. Bartley, S. Bulger, L. Burrell, M. Combes, D. Conwell, C. Edds, K. Edds, M. Fillmore, E. Finck, P. Fillmore, E. Greer, J. Halstead, T. Hirata-Edds, W. Jensen, P. Lamberson, D. Mulhern, M. Nelson, D. Papoulias, C. Pendergraft, L. Scott, C. Wilkinson, and J. Witters, J. Whitaker, D. Zumwalt, and the City of Emporia. Funding was provided by the Emporia State University Department of Biological Sciences, and by the U.S. Army Corps of Engineers through a National Biological Service cooperative agreement (No. 14-45-CA03-97-908).

#### LITERATURE CITED

- Bowen, C. A., Jr. 1980. The life history of the brindled madtom *Noturus miurus* (Jordan) in Salt Creek, Hocking and Vinton counties, Ohio. M.S. thesis, Ohio State University, Columbus. 195 pp.
- Breder, C. M., Jr. and D. E. Rosen. 1966. Modes of reproduction in fishes. The Natural History Press, Garden City, New York. 941 pp.
- Bulger, A. G. 1999. Population structure, habitat use, and breeding behavior of the Neosho madtom, *Noturus placidus*. M.S. thesis, Emporia State

- University, Emporia, KS. 83 pp.
- Bulger, Angela and David Edds. 2001. Population structure and habitat use in Neosho madtom (*Noturus placidus*). *Southwestern Naturalist* Vol. 46:1.
- Burr, B. M. and R. L. Mayden. 1982. Life history of the freckled madtom, *Noturus nocturnus*, in Mill Creek, Illinois (Pisces: Ictaluridae). *Occas. Pap. Mus. Nat. Hist. Univ. Kans.* 98:1-15.
- Chan, M. D. 1995. Life history and bioenergetics of the brown madtom, *Noturus phaeus*. M.S. thesis, University of Mississippi, Vicksburg. 177 pp.
- Clark, K. E. 1978. Ecology and life history of the speckled madtom, *Noturus leptacanthus* (Ictaluridae). M.S. thesis, University of Southern Mississippi, Hattiesburg. 134 pp.
- Cochran, P. A. 1996. Cavity enhancement by madtoms (genus *Noturus*). *J. Freshwater Ecol.* 11:521-522.
- de Vlaming, V. L. 1972. Environmental control of teleost reproductive cycles: a brief review. *J. Fish Biol.* 4:131-140.
- Dinkins, G. R. and P. W. Shute. 1996. Life histories of *Noturus baileyi* and *N. flavipinnis* (Pisces: Ictaluridae), two rare madtom catfishes in Citico Creek, Monroe County, Tennessee. *Bul. Ala. Mus. Nat. Hist.* 18:43-69.
- Fitzpatrick, K. C. 1981. Comparative reproductive behavior of the slender (*Noturus exilis*), brindled (*N. miurus*) and freckled (*N. nocturnus*) madtoms (Pisces: Ictaluridae). M.S. thesis, Southern Illinois University at Carbondale, Carbondale. 66 pp.
- Jobling, M. 1995. Environmental biology of fishes. Chapman and Hall, New York. 455 pp.
- Matthews, W. J. 1998. Patterns in freshwater fish ecology. Chapman and Hall, New York. 756 pp.
- Mayden, R. L. and B. M. Burr. 1981. Life history of the slender madtom, *Noturus exilis*, in southern Illinois (Pisces: Ictaluridae). *Occas. Pap. Mus. Nat. Hist. Univ. Kans.* 93:1-64.
- Östlund S. and I. Ahnesjö. 1998. Female fifteen-spined sticklebacks prefer better fathers. *Animal Beh.* 56:1177-1183.
- Pfingsten, D. G. and D. R. Edds. 1994. Reproductive traits of the Neosho madtom, *Noturus placidus* (Pisces: Ictaluridae). *Trans. Kans. Acad. Sci.* 97:82-87.
- Starnes, L. B. and W. C. Starnes. 1985. Ecology and life history of the mountain madtom, *Noturus eleutherus* (Pisces: Ictaluridae). *Amer. Midl. Nat.* 114:331-341.
- Sundararaj, B. I. and A. Sehgal. 1970. Effects of a long or an increasing photoperiod on the initiation of ovarian recrudescence during the preparatory period in the catfish, *Heteropneustes fossilis* (Block). *Biol. of Reprod.* 2:413-424.
- U. S. Fish and Wildlife Service. 1991. Neosho madtom recovery plan. U.S. Fish and Wildlife Service, Denver, Colorado. 42 pp.
- Wilkinson, C. and D. Edds. 1997. Breeding biology of the Neosho madtom, with assessment of population status and habitat use in the Cottonwood and Neosho rivers of Lyon and Chase counties, Kansas. Report to Kansas Department of Wildlife and Parks, Pratt. 63 pp.
- Wootton, R. J. 1990. Ecology of teleost fishes. Chapman and Hall, London. 404 pp.