INFLUENCE OF FLOWING WATER ON NEOSHO MADTOM (*NOTURUS PLACIDUS*) REPRODUCTIVE BEHAVIOR

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TABLE OF CONTENTS

LIST OF TABLES iii

LIST OF ILLUSTRATIONS iv

ABSTRACT v

INTRODUCTION 1

METHODS 3

Experimental Design

Data Collection

Reproductive Behaviors

Analysis

RESULTS 10

Overall Flow Effects

Behavior Sequences

Parameter Patterns through Time

DISCUSSION 13

SUMMARY 17

ACKNOWLEDGEMENTS 18

BIBLIOGRAPHY 19

APPENDIX

TABLES 26

FIGURES 36

LIST OF TABLES

Table Page

1. Summary of two summers when water flow experiments occurred 27

2. Neosho madtom ethogram 28

3. Summary of proportion of time, frequency, and bout length of behaviors for the first summer 29

4. Summary of proportion of time, frequency, and bout length of behaviors for the second summer 30

5. Summary of the true probability values from different treatments using permutation techniques 31

6. Summary of the significant relationships found in male fish using sequential analysis 32

7. Summary of the significant relationships found in female fish using sequential analysis 33

8. Summary of the permutation tests for autocorrelation 34

9. Summary of patterns over time for reproductive behaviors 35

LIST OF ILLUSTRATIONS

Figure		Page
1.	Neosho madtom (*Noturus placidus*)	37
2.	Neosho madtom distribution	38
3.	Experiment tank setup showing nest site and recirculating apparatus...	39
4.	View of side camera used both summers	40
5.	A male Neosho madtom engaged in nest building behavior	41
6.	A pair of fish engaged in the jostle behavior	42
7.	A pair of fish engaged in the carousel behavior	43
8.	A pair of fish engaged in the embrace behavior	44
9.	Neosho madtoms spawning	45

ABSTRACT

Recent research has concluded that flowing water could be beneficial in catfish reproduction. If flowing water is instrumental to reproducing catfish in the laboratory then river flow modifications from dams could impact the reproduction of one specific catfish species, the Neosho madtom (*Noturus placidus*). The Neosho madtom is a small short-lived species that is endemic to the gravel bars of the Neosho River. It excavates a nesting cavity in the gravel and spawns during the summer. This species has survived initial dam construction within the Neosho River basin but with adequate declines to be added to the federal threatened species list in 1990. To examine whether flowing water affects Neosho madtom reproductive behaviors I conducted a laboratory experiment using aquaria with and with out flowing water. Overall flowing water decreased the average frequency, proportion of time, and bout length of nest building behavior. Reproductive behavior sequences that included embrace also were negatively impacted by flowing water, although no distinct patterns of reproductive behaviors were seen through time. Because these behaviors are essential to the courtship and reproduction in the Neosho madtom, altering the flow regime could affect overall reproductive success if water flow during the spawning season was unusually high. This could have a major impact on the Neosho madtom which only spawns once or twice during its lifespan.

INTRODUCTION

Many environmental cues trigger spawning in temperate fish species including food abundance, photoperiod, temperature, floods, lunar cycles, and social interaction (Bye 1984, Munro et. al 1990). These cues can differ from family to family and even between closely related species depending upon geographical range and the dominant environmental conditions (Bye 1984). Within the family Ictaluridae, temperature, photoperiod, and flowing water have all been suggested as an environmental trigger for spawning (Brauhn 1971, Brauhn and McCraren 1975, Vasal and Sundararaj 1976, Davis et. al 1986, and Kelly and Kohler 1996, Stoeckel and Burr 1999). This association between flowing water and the reproductive cycle also seems plausible in another catfish genus, *Noturus*. This genus comprises 25 species mostly found in well oxygenated environments and fast riffle areas of North American warmwater streams (Taylor 1969, Burr and Stoeckel 1999).

Altering the annual water flow regime of a river can affect spawning fish and their overall reproductive success. When discharge mimics the natural river flow effects are positive in striped bass (*Morone saxatilis,* Zincone and Rulifson 1991) and lake sturgeon (*Acipenser fulvescens,* Auer 1996). When dam discharge is modified, negative effects occur to spawning fish and their success including impeding upstream migration to spawning grounds (Votinov and Kas'yanov 1978), decreasing the nutritional state and growth of fry (Gomes and Agostinho 1997), and decreasing the growth and survival of eggs and fry (Reiser and White 1990).

For one species of *Noturus*, the Neosho madtom (*Noturus placidus*, Figure 1), numerous low-head and large flood control dams have been constructed within this species range in the Neosho River basin (Tulsa District U.S. Army Corps of Engineers 1993, Figure 2). Research has found that one of these flood control dams has decreased the magnitude of peak discharge (Studley1996, Wildhaber et al. 2000), lowered the minimum flow (Wildhaber et al. 2000), and increased substrate size (Wildhaber et al. 2000). These studies indicate water flow modifications can indirectly affect the Neosho madtom but the direct effects of flowing water are not fully understood.

Five species of madtoms are listed as threatened or endangered by the U.S. Fish and Wildlife Service (Burr and Stoeckel 1999) including the Neosho madtom (U. S. Fish and Wildlife 1991). A typical sized wild adult Neosho madtom is 35-70 mm (Fuselier and Edds 1994, Edds 1995, Bulger and Edds 2001), which is about one-fourth the size of the largest species of madtom, the stonecat (Trautman 1981, Etnier and Starnes 1993). One reason for the small size is the short lifespan, common to most madtom species (Burr and Stoeckel 1999). The oldest Neosho madtom found has been three years with most collected as one and two-year olds (Moss 1981, Bulger and Edds 2001). Like most madtoms, Neosho madtoms are mostly found in gravel bars along mainstem rivers in the Neosho River basin (Taylor 1969, Moss 1981, Moss 1983, Wilkinson and Edds 1997, Bulger 1999). Nests are constructed under large objects in the gravel where spawning occurs (Wilkinson and Edds 1997, Bulger 1999). Reproduction in Neosho madtoms is especially important because spawning events are limited to one, maybe two, spawning events for each female fish (Bulger and Edds 2001). Male parental care is dominant in this genus with very few observations of female parental care (Burr and Stoeckel 1999)

and Neosho madtoms are no exception with only male parental care being observed and lasting 8-9 days after spawning (Wilkinson and Edds 1997, Bulger 1999).

To fully understand whether flowing water directly affects Neosho madtom reproduction we conducted a laboratory study examining Neosho madtom reproductive behavior under flow and non-flow conditions. We chose to study reproductive behaviors over other indicators of reproduction because of specific limitations associated with this species. First, numbers for collecting Neosho madtoms are limited due to their threatened status, so sacrificing fish to acquire gonadal information is not possible. Second, reproductive behaviors would indicate the amount of potential reproduction in this species due to complex courtship behaviors (Fitzpatrick 1981, Bowen 1980, Chan 1995, Bulger 1999). Third, overall spawning success is almost impossible to examine in the Neosho River due to turbidity (Moss 1981, Edds 1995) and due to the lack of laboratory success at spawning madtoms (Bulger 1999, Stoeckel and Burr 1999).

METHODS

Experimental Design

During two summers, an experiment involving flowing water and non-flowing water aquaria (Table 1) was conducted at the U. S. Geological Survey Columbia Environmental Research Center, Columbia, Missouri. This experiment examined the effects of flowing water on the reproductive behaviors of the Neosho madtom. The flow treatment aquaria were equipped with a water recirculating apparatus (Figure 3). In the flow aquaria, velocities were set to similar levels found at Neosho madtom collection

sites during the spawning season (~30 cm/sec, Wilkinson and Edds 1997). The non-flow treatment aquaria had the same set up but lacked the water pump (located outside the aquaria) creating static aquaria.

The Neosho madtoms used in this study were collected from the Cottonwood and Neosho rivers during the summer of 1998 (Figure 2) and kept in the laboratory throughout. This laboratory environment mimicked the natural photoperiod and temperatures normally found in the Neosho River and at the latitude and longitude of Kansas (N 38° 26 min., W 96° 12 min., Wilkinson and Edds 1997, Bulger 1998, U. S. Naval Observatory 1999-2001). The light period (8-16 hr) and temperature (9-27°C) were continually modified throughout the year to reflect natural cycles which included an overwintering period where temperatures decreased to 9°C and the photoperiod to 8 hr of light. Transitions between light and dark were immediate. Neosho madtoms are nocturnal (Moss 1981, Bulger 1999), and those in the lab acclimated to the point of anticipating the lighting changes, immediately becoming active as soon as the lights were turned off. The experiment was conducted corresponding to the natural summer spawning season of Neosho madtoms (Pfingsten and Edds 1994, Bulger 1999). Changes in temperature and photoperiod induced gonad production and secondary sexual characteristics common to madtoms (Taylor 1969, Clark 1978, and Mayden and Burr 1981). Specifically, the external physical characteristics of spawning males include enlarged cephalic epaxial head muscles and swollen lips. Females do not have swollen head muscles or lips like the males but have extended abdomens due to egg production. Both sexes exhibit swollen genital papillae and specific to the Neosho madtoms, reddened tooth patches (Pfingsten and Edds 1994, Bulger 1999). Fish with obvious

secondary sexual characteristics were chosen for the experiment and male/female pairs of madtoms were randomly assigned to a flow or non-flow treatment aquaria.

During the experiment, temperature and photoperiod were modified using Aquarium Systems Visi-Therm aquarium 300W heaters and a light timer. Changes of 15-20 minutes per week in photoperiod continued until the maximum of 16 hr of light. An increase of one degree Celsius in temperature per week continued until a maximum of 27°C. The experiment continued until there were no more signs of spawning activity; the first summer the experiment lasted 63 days while the second summer only lasted 44 days (Table 1). During the experiment, the turnover rate of fresh water in the aquaria was changed due to the minimal heating capacity of the heaters. At low temperatures (19-21°C) one aquarium water exchange occurred 1.88 times a day, temperatures between 22 and 25°C water exchanged 0.053 aquaria per day, and above 25°C water exchanged 0.026 aquaria per day. Food was fed ad labitum three times a week and excess food was removed to prevent disease. Food included: frozen brine shrimp, frozen bloodworms, and Hikari Sinking Carnivore Pellets.

Data Collection

Because Neosho madtoms are nocturnal (Moss 1981, Bulger 1999), reproductive behaviors were documented using time-lapse video recorders and infrared lights. During each experiment, 24-hr continuous video recordings were collected using two different camera views. For each year Panasonic WV-BP310 black and white cameras were positioned directly in front of the aquaria and gave a side view of the entire aquarium (Figure 4). The second year an additional camera, Micro Video Products MVC 2000-

WP-LED, was positioned inside the aquaria directly above the nest (Figure 5-9). This allowed for a more detailed view of the nest and the spawning behaviors and verified the behaviors seen in the side view.

For the analysis only nighttime video was used due to low levels of activity during the day. Nights with disruptions were excluded due to the potential for stress-induced behavior or lack of data (disruptions involved feeding, power failure, and recording failure). Due to the time involved with quantifying the video recordings the use of all possible nights was impractical so the video-tapes were subsampled. A random sample of 17 nights per aquaria was selected because it represented approximately 50% of the undisturbed nights. During the night, a random five-minute period was used to represent each hour. During this random five-minute period each fish was followed separately and the initial time of every behavior was recorded along with the position of the fish in the aquaria (i.e. in/out of the nest).

For each behavior the proportion of time (during a five-minute period), frequency (frequency during a five-minute period) and average bout length (frequency divided by the total time of occurrence in seconds during a five-minute period) was calculated using SAS (1990). Each mean was calculated by first averaging the parameter per fish (i.e. two fish per aquaria) during each five-minute period then averaging over the day and finally the entire experiment. This average also included every hour and day the behavior did not occur (i.e. zero proportions).

Reproductive Behaviors

The Neosho madtom ethogram used in this study was modified from research done by Bulger (1999) and contained 15 different behaviors. Only 11 out of the 15 behaviors were seen during data collection (Table 2). Five of these 15 behaviors are considered important in reproduction: nest building (Figure 5), jostle (Figure 6), carousel (Figure 7), embrace (Figure 8), and spawning (Figure 9). Even though no spawning occurred during the experiment, spawning during the subsequent year and previous madtom studies (Fitzpatrick 1981, Stoeckel 1993, Chan 1995, and Bulger 1999) have shown these reproductive behaviors occur during spawning. The four reproductive behaviors observed during the experiment (nest building, jostle, carousel, and embrace) were used in testing the effects of water flow on Neosho madtom reproductive behavior.

Analysis

Overall treatment effects on individual behaviors and their corresponding parameters (frequency, bout length, and proportion of time) were assessed using multiresponse permutation procedures (BLOSSOM Version W2001.05a, Cade and Richards 2000), which is equivalent to multivariate analysis of variance tests. The use of permutation tests were necessary due to the numerous zeros in the data set which made the assumptions of normal distribution and constant variance, associated with parametric statistics, unobtainable. Permutation techuiques use the actual distribution of the data and calculate the true probability of occurrence unlike parametric tests, which calculate probabilities using a normal distribution. The only assumption needed in permutation tests is independence. To test differences BLOSSOM (Cade and Richards 2000) uses

rerandomization of each separate data point and then calculates the distances between all points at each rerandomization step. The extent of these permutations is dependent on sample size. From these distances it then compares the observed intragroup distances to all possible intragroup distances and calculates the probability that the observed distances could be smaller based on the set of all possible distances, which is weighted by relative sample size. Prior to using BLOSSOM, differences between the years were adjusted for by alignment (Mielke and Iyer 1982). This procedure literally aligns the data by taking the average of each year and then subtracting that average from each observation within that year. Alpha was set at 0.05.

The patterns of each individual reproductive behavior were analyzed using the lag sequential method (Gottman and Bakeman 1979, Sackett 1979, and Sackett 1980). This type of analysis examines the order in which the behaviors occurred and compares observed probability to the expected probability. The order of the sequence is designated by given (initial behavior of interest) and target behaviors (final behavior of interest) where the given behavior is first and then the target behavior occurs from one to three steps or lags after. Within each sequence the behaviors that occur between the target and given behavior are random. All possible reproductive behavior pairwise comparisons and lags were tested using the Pearson chi square test in GSEQ for Windows (Bakeman and Quera 1995). To assess significant differences a Bonferroni adjusted alpha level was used (0.05/64 comparisons = 0.0008).

Since the experiments happened over time, patterns of the three reproductive behavior parameters through time were examined using regression analysis. Each week was treated as one group because the photoperiod and temperature changes occurred once

a week. The two summers of experiments were first shifted using temperature so the weeks with the same temperature were assigned the same week number. Due to the later start of the second summers experiment the first week did not contain any observations (Table 1). The frequency, average bout length and proportion of time spent engaged in all reproductive behaviors (nest building, jostle, carousel, embrace) were averaged over the respective aquaria and weeks for each summer and then all reproductive behaviors were summed to examine overall reproductive patterns through time. Due to random sampling, not all aquaria were sampled each week so the numbers of observations for each week were similar but not the same. Numerous zeros prohibited the ability to normalize the data so permutation versions of the Durban Watson test and regression analysis were used. When a pair of fish had five or more consecutive weeks sampled they were examined with the multiresponse sequence procedure in BLOSSOM (Version W2001.05a, Cade and Richards 2000). This procedure tests for first-order serial dependency on univariate or multiresponse variables. In general, this procedure tests the average distance between the ordered observations to the average distance off all possible random pairs of observations. The alpha level was adjusted using a Bonferroni corrected p-value since BLOSSOM cannot incorporate all data layers at once (alpha 0.05/4 = 0.0125, 4 = 2 summers x 2 treatments).

After the values are tested for independence they were then tested for three possible patterns over seven weeks (linear, quadratic, and cubic). In order to do this the differences between years and treatment are removed before using BLOSSOM by alignment procedure (Mielke and Iyer 1982). This procedure literally aligns the data by taking the average of each year and treatment combination, then subtracting that average

from each observation within that year/treatment combination. If these effects cannot be removed then the data is separated into the individual year treatment groups and parallel analysis were conducted on each group. These parallel analyses involve the Least Absolute Deviation Regression procedure (LAD) in BLOSSOM (Version W2001.05a, Cade and Richards 2000). This procedure is equivalent to parametric linear regression analysis but instead of calculating the sum of the squared deviation it calculates the absolute sum and consequently computes true probabilities. When analyzing for polynomial regression BLOSSOM compares the proportionate reduction in the sums of absolute deviations when passing from a reduced to full parameter model. For example the reduced model would be one that only contains the linear variable, where a full parameter model would contain the linear and quadratic variables. The corresponding least absolute deviation regression coefficient of determination was calculated using the full verses reduced model sum of absolute deviations (Cade and Richards 1996, Cade 1997). The overall alpha level was adjusted using Bonferroni correction since BLOSSOM cannot incorporate all data layers at once (alpha 0.05/12 = 0.0042, 12 = 2 summers x 2 treatments x 3 different tests).

RESULTS

Overall Flow Effects

On average, swimming and resting were the two most common behaviors in either treatment (Table 3 and 4). Scratching, chase, parallel swim display, and mouth bite were not seen during the experiment regardless of treatment so they were dropped from

the analysis. The vast majority of the reproductive behaviors occurred in the nest (Table 5) and the treatment did not seem to affect the percentage.

In general the first summer had more overall activity including reproductive behaviors consequently there was a significant difference between the years (Table 6), which incorporates not only the increased age in the fish but also modifications of the aquaria (Table 1). Prior to using BLOSSOM the significant difference between the years was adjusted for by alignment (Mielke and Iyer 1982). This alignment procedure did remove the difference between the years (Table 6). These aligned observations were then tested for flow effects.

When all behaviors were examined the only behavior that was affected by flowing water was nest building (Table 6). Nest building decreased in the proportion of time, frequency, and average bout length in the flowing water treatment. When examining only the reproductive behaviors flowing water decreased the proportion of time and freqnency of nest building but increased the proportion of time of jostle which increased the average proportion of time of the combination of the three main reproductive behaviors (jostle, carousel, and embrace, Table 6).

Behavior Sequences

Sequential analysis also found flowing water had an effect on reproductive behaviors (Table 7 and 8). The analysis was done separate for males and females but because the majority of the reproductive behaviors involve both fish (e.g. jostle, carousel, and embrace) the results were similar and male results will only be discussed (Table 7).

Overall, the sequential analysis found nest building was minimally associated with the other behaviors. In general, once nest building occurs it tends to be followed by more nest building, which is evident in the greater than expected sequences of nest building with nest building two and three lags after. Flowing water negatively impacted only one nest building sequence in the study, which involved nest building with embrace one lag after.

In contrast, the three other reproductive behaviors (jostle, carousel and embrace) had the majority of the positive relationships. Almost all of the sequences beginning with jostle occurred more than expected. Flowing water affected two sequences beginning with jostle: jostle to embrace one and three lags after. The only sequence that did not show any relationship was jostle with carousel two lags after. As for sequences starting with carousel, most relationships were positive. The only carousel sequence that did not show any relationship was carousel with embrace two lags after. Sequences with embrace as the given behavior were all positive except for those involved with nest building. Flow affected one sequence, embrace with jostle two lags after. Overall, flowing water impacted four sequences, all involved embrace including the only negative association among all the sequences.

Parameter Patterns through Time

Of the aquaria that data were collected at least 6 weeks in a row (12 out of 18), none showed significant autocorrelation between the weeks, which means the weekly values for each pair of fish were not related (Table 9). Because the weekly values were independent all 18 aquaria were then used to examine the patterns of the three

reproductive behavior parameters through time. There was a significant year and treatment effect that could not be removed using the alignment procedure. Each individual year/treatment data set was analyzed for patterns through time using LAD procedure in BLOSSOM. Only one of the year/treatment combinations exhibited any pattern through time (summer 1, nonflow treatment) and only involved two parameters (Table 10). The frequency and the proportion of time of all reproductive behaviors in the first summers nonflow treatment aquaria increased through time with a quadratic pattern.

DISCUSSION

The fish used in this study were two and three years old which is longer than the expected life span of wild Neosho madtoms (Moss 1981, Bulger 1999). This extension of the life span was likely due to the lower stress environment of the lab and the lack of other stress factors such as predation. However, the advanced age did not prohibit the performance of reproductive behaviors. Both male and female Neosho madtoms exhibited nest building behaviors. This is consistent with other researchers who have observed male and/or female madtoms moving rocks and creating depressions in gravel (Fitzpatrick 1981, Stoeckel 1993, Chan 1995, Wilkinson and Edds 1997, and Bulger 1999). The jostle has only been described and observed in this study and one previous Neosho madtom study (Bulger 1999). Both of these studies are the only ones that have incorporated videotaping of the behaviors versus direct observations. Video is more advantageous than direct observation due to minimized observer induced response, continuous monitoring, and the ability to rewind and review the behaviors repeatedly.

In general, this study found a decrease in the frequency, bout length, and the proportion of time engaged in nest building behavior of Neosho madtoms. Nest building was the most impacted behavior likely due to the energetic costs associated with moving rocks by nudging or carrying them in the mouth. Despite its potentially high energetic cost, nest building is a very important aspect in madtom reproduction because the nest is the site of extended activity (Chan 1995, Wilkinson and Edds 1997, Bulger 1999). Extended pre-spawn reproductive activity occurs with as much as 3 weeks of post-spawn parental care for the eggs and young. The nest is shelter from predators not only for the spawning pair but the eggs and young (Mayden et al. 1980 and Mayden and Burr 1981). Researchers who have disturbed nests containing eggs have found them predated soon after discovery.

This negative impact of flowing water on nest building behavior observed in this study indicates that different flow regimes from flood control dams could impact this behavior and possibly reproductive success. If the outflow from the dam is unusually high during the spawning season compared to normal flow this could potentially limit the amount of nest building activity and consequently have an overall negative impact on spawning. Wildhaber et al. (2000) found the flow regime below the John Redmond Dam and John Redmond Reservoir has an increased long-term (30-day and 90-day) maximum flows, increased length and variability in length of high-flow events, and has a delayed and more variable date of maximum annual flow. These increases in the flow regime are consistent with the purpose of the dam (i.e. flood control) which holds back as much water as possible during the spring flood pulse while releasing the maximum allowed so the river flows as much as bank-full for weeks instead of days. This extension of

maximum flows into the summer Neosho madtom spawning season (Bulger and Edds 2001) could negatively impact their reproductive success by decreasing the amount of nest building activity.

Wildhaber et al. (2000) also found that the Neosho River below John Redmond dam has lower minimum flows, lower short-term (1-day and 3-day) maximum flows, increased occurrence of low-flow events and much less variability in flow rates. These altered flow regimes could have an indirect effect on the reproductive activity especially nest building by modifying the substrate in which madtoms live and build their nests. The occurrence of loose unconsolidated gravel substrate is important to Neosho madtom distribution (Fuselier and Edds 1994, Bulger and Edds 2001) and with the decrease in flows can expose more gravel to cementation. Cementation is the process of hardening of the gravel after exposure to extended dry periods (Deacon 1961) and has been suggested as a negative impact on this species (Deacon 1961, Cross and Moss 1987, Wildhaber et al. 2000). These changes in habitat could indirectly impact Neosho madtom reproduction by confounding the decrease in nest building behavior with the lack of suitable nest building habitat.

The lack of negative impacts involving nest building behavior in the sequential analysis compared to the overall analysis is most likely due to scale. Only lags 1-3 were examined which means only behaviors occurring no more than three steps from the given behavior were included in the analysis. This could eliminate behaviors such as nest building, which can occur days before any carousel is observed (Fitzpatrick 1981, Chan 1995). The lack of proximity to reproductive behaviors does not mean nest building is not important since most spawns in the lab occurred in nests, egg masses have only been

found in the wild in nests, and for almost all species in the genus *Noturus* some kind of cover is used for nesting (Burr and Stoeckel 1999).

Carousel and embrace has been described during the spawning of Neosho, brindled (*N. miurus*), freckled (*N. nocturnes*) and margined madtoms (*N. insignis*, Fitzpatrick 1981, Stoeckel 1993, Bulger 1999) however only embrace was observed in the spawning of brown madtoms (*N. phaeus*, Chan 1995). In these studies, spawning was only observed after carousel and embrace. In the sequential analysis we found that differences between flow and non-flow aquaria involved embrace sequences that lacked positive relationships. The decrease in embracing could lead to overall lower reproduction because spawning occurs during this behavior (Fitzpatrick 1981, Stoeckel 1993, Chan 1995, Bulger 1999).

Overall, the lack of patterns associated with the flow treatment aquaria indicates the lack of overall reproductive activity due to flowing water. The only patterns found were during the first summer and only in the nonflow aquaria. This lack of significant patterns indicates the amount of reproductive activity was constant throughout the spawning period. This suggests that once the environmental conditions are favorable the fish exhibit spawning behavior for weeks. This extended effort would be expected in a species that only spawns once maybe twice (Bulger and Edds 2001). These favorable conditions due fluctuate and the length of the spawning period does change over the years depending on conditions (Bulger and Edds 2001).

The specific negative impacts of flowing water found in this study can be amplified due to other life history aspects, characteristic of not just Neosho madtoms but all madtoms. There is limited amount of spawning opportunities for each fish due to a

short life span and the limited number of eggs per female (Burr and Stoeckel 1999, Bulger and Edds 2001). Consequently, each spawning season is crucial, especially when numbers are already low and one low producing year could have detrimental effects on the overall population. Since madtoms are not suspected to migrate considerable distances (Burr and Stoeckel 1999) these low producing years could also mean local extirpation.

SUMMARY

Overall, flowing water does impact reproductive behavior in Neosho madtoms including negative impacts on nest building, carousel and embrace behaviors. These impacts are further confounded by this species' inherent life history characteristics and the habitat with which they are associated. The management of the dams in the Neosho River basin potentially impacts Neosho madtom reproductive behavior and the substrate where nests are built. Reducing the magnitude of flows during the spawning season but allowing flows large enough to enhance, not deteriorate the substrate, could lessen these impacts. This water flow level is currently unknown but other dams that discharge flow regimes similar to the natural flow regime have had positive effects on other fish species (Zincone and Rulifson 1991, Auer 1996). This natural flow regime strategy should be considered as often as possible to limit the negative impacts of modified flow regimes on the Neosho madtom population.

The applicability of these results to natural populations of Neosho madtoms and other species of madtoms can only be suggestive at the present; more research is needed.

The lack of multiple water velocities tested in this study limits the scope of the study as to the relative impacts of water flow on behaviors. A more complex study involving several different water velocities would help to understand the more complex impacts of flowing water on reproductive behaviors. A more comprehensive stream survey of different habitats and their relationship to water flow and madtom distribution would link the information found in lab studies to practical applications in flood control dam management.

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APPENDIX
TABLES

Table 1. Summary of the two summers that water flow experiments occurred.

	Summer 1 (1999)	Summer 2 (2000)
Number of observations	12	6
Aquaria size	21.88 L	43.72 L
Camera used	side view	side view and top view
Days sampled per aquaria	17	17
Length	started 5/22/99 ended 7/25/99	started 6/03/00 ended 7/18/00
# of days sampled	35 out of 63	25 out of 44
Turnover rate per day	0.026 - 1.88 aquaria	0.026 - 1.88 aquaria
Starting photoperiod	14.3 hr	15.25 hr
Starting temperature	19°C	20°C

Table 2. Neosho madtom ethogram (modified from Bulger 1999)

Swimming: Fish is moving around the tank. This could include circling on the glass or moving around on the bottom of the aquarium where the fishes movements are only to propel itself through the water.
Feeding: Fish is searching or eating food including nudging with the mouth around in the gravel spaces and then with mandibular movements eating the food found in the gravel.
Resting: Fish is not moving, usually sitting on the bottom.
Scratching:[1] Fish rubs on an object with a part of its body.
Nudge: Fish swims up to other fish and bumps or touches it with its head.
Oral Flare: Fish opens mouth and flares its opercula directing this display toward the other fish.
Chase:[1] Fish swims close behind the other fish, following it around the tank.
Parallel Swim Display:[1] Fish are positioned parallel to each other, spread their fins, and move their bodies in a sigmoid shape, forcing strong currents of water toward the other fish.
Bite: Fish inserts a part of the other fish into its' mouth and closes it.
Mouth Bite:[1] Fish uses it's mouth to clasp onto the other fishes mouth and the two fish swim back and forth while they are clamped by the mouth with each other.
Nest Building:[2] Nest building is distinguished in madtoms by creating a cavity under an object. This object could be a rock, bottle, can, or in this experiment a piece of PVC. Fish moves rocks by using its' head as a shovel and pushing the rock or by picking the rock up in its' mouth and carrying it outside the nest.
Jostle:[2] Fish is in constant contact with the other fish, facing the same direction. Both fish swim up and down and side to side, and switch positions continually.
Carousel:[2] Fish swims up beside the other fish, head to tail. This fish bites/nudges the other fish in the caudal peduncle area, and both fish swim in a circular pattern, head to tail.
Embrace:[2] Fish is located beside the other fish, head to tail. One or both fish curls its caudal fin around the other fish's head.
Spawning:[1,2] Fish release gametes.

[1] Indicates behavior that did not occur during data collection, consequently no analysis could be done.
[2] Indicates reproductive behavior.

Table 3. Summary of the proportion of time, frequency, and bout length (averaged per five minute period) of the behaviors observed during the first summer (n = 12).

	Proportion of Time			Frequency			Bout Length		
Flow	Average	Range		Average	Range		Average	Range	
Swimming	0.7098	0.4286	0.8115	2.6475	1.6890	4.6918	127.4470	30.6170	187.9860
Feeding	0.0004	0	0.0010	0.0089	0	0.0252	0.1700	0	0.4202
Resting	0.1952	0.1268	0.3437	1.3979	0.8322	2.4014	34.2510	22.6491	49.3193
Nudge	0.0012	0.0005	0.0020	0.1190	0.0358	0.2498	0.5155	0.2557	0.7916
Mouth Flare	0	0	0	0	0	0	0	0	0
Bite	4.1×10^{-6}	0	2.5×10^{-5}	0.0012	0	0.0074	0.0012	0	0.0074
Nest Building	0.0097	0.0041	0.0162	0.1429	0.0514	0.2929	3.5096	1.5134	5.0643
Jostle	0.0246	0.0054	0.0447	0.4759	0.0655	1.1397	3.1471	0.6836	5.3117
Carousel	0.0253	0.0003	0.0717	0.4426	0.0065	1.2839	2.8454	0.0915	7.6127
Embrace	0.0337	0.0007	0.0936	0.2833	0.0131	0.7544	5.4045	0.1961	15.1944
Non-flow									
Swimming	0.7072	0.5419	0.8991	3.1964	1.7646	4.1996	114.1360	58.3580	202.2820
Feeding	0.0002	0	0.0012	0.0056	0	0.0252	0.0724	0	0.3838
Resting	0.1884	0.0993	0.2478	1.1362	0.6089	1.8042	38.2059	24.6348	43.8551
Nudge	0.0011	0.0002	0.0027	0.0692	0.0173	0.1284	0.4707	0.0836	1.2997
Mouth Flare	9.3×10^{-6}	0	5.6×10^{-5}	0.0007	0	0.0042	0.0056	0	0.0336
Bite	9.8×10^{-5}	0	0.0006	0.0006	0	0.0037	0.0588	0	0.3529
Nest Building	0.0220	0.0008	0.0431	0.4066	0.0069	0.7007	5.5362	0.4804	10.0387
Jostle	0.0225	0	0.0393	0.6226	0	1.2353	2.6250	0	4.9468
Carousel	0.0285	0	0.0528	0.5900	0	1.2185	3.1485	0	6.0500
Embrace	0.0301	0	0.1004	0.3450	0	0.6723	4.6648	0	15.9212

Table 4. Summary of the proportion of time, frequency, and bout length (averaged per five minute period) of the behaviors observed during the second summer (n = 6).

	Proportion of Time			Frequency			Bout Length		
Flow	Average	Range		Average	Range		Average	Range	
Swimming	0.6245	0.4365	0.8297	3.6353	2.4506	4.7011	75.2783	30.5590	136.1050
Feeding	0	0	0	0	0	0	0	0	0
Resting	0.3698	0.1688	0.5552	2.6097	1.5050	3.7805	53.7481	39.3704	64.2348
Nudge	0.0036	0.0010	0.0064	0.2513	0.0830	0.3899	1.1560	0.3946	2.0569
Mouth Flare	4.7×10^{-6}	0	1.4×10^{-5}	0.0014	0	0.0042	0.0028	0	0.0084
Bite	0	0	0	0	0	0	0	0	0
Nest Building	0.0001	0	0.0002	0.0053	0	0.0158	0.0487	0	0.1460
Jostle	0.0020	0.0005	0.0035	0.0487	0.0242	0.0735	0.3839	0.1261	0.6747
Carousel	0.0001	0	0.0002	0.0028	0	0.0084	0.0168	0	0.0504
Embrace	6.7×10^{-5}	0	0.0002	0.0028	0	0.0084	0.0196	0	0.0588
Non-flow									
Swimming	0.5830	0.3911	0.8270	3.4452	2.8281	3.8199	79.9287	40.2880	141.3960
Feeding	0	0	0	0	0	0	0	0	0
Resting	0.3369	0.1716	0.4220	2.3909	1.8343	2.8640	45.7556	19.6552	64.5027
Nudge	0.0032	0.0014	0.0059	0.2344	0.1475	0.3073	1.3163	0.5823	2.3794
Mouth Flare	5.7×10^{-5}	0	0.0001	0.0123	0	0.0332	0.0344	0	0.0885
Bite	1.9×10^{-5}	0	5.6×10^{-5}	0.0014	0	0.0042	0.0112	0	0.0336
Nest Building	0.0081	2.8×10^{-5}	0.0174	0.1393	0.0042	0.3083	2.1300	0.0168	4.6249
Jostle	0.0382	0	0.0844	0.6703	0	1.5247	3.9128	0	8.4567
Carousel	0.0081	0	0.0204	0.2808	0	0.6450	1.3692	0	3.5789
Embrace	0.0224	0	0.0588	0.2234	0	0.5410	4.2567	0	11.1443

Table 5. Summary of the true probability values from treatment tests using permutation techniques. The lowest possible p-value was 0.00005 due to a sample size of 18 (alpha = 0.05).

	p-value		
Block effect	Frequency	Bout length	Proportion of time
active behaviors	0.0234*	0.0283*	0.0419*
After alignment			
active behaviors	0.9808	0.9844	0.9729
Overall behaviors			
resting	0.4937	0.6016	0.7088
active behaviors	0.1870	0.1698	0.1662
swimming	0.5636	0.7785	0.7728
feeding	0.6084	0.3060	0.4039
nudge	0.2991	0.6676	0.7023
oral flare	0.6579	0.3158	0.3158
bite	1	0.6199	0.6199
nest building	0.0088v	0.019v	0.0095v
jostle	0.2026	0.7321	0.4566
carousel	0.3640	0.4332	0.4974
embrace	0.5085	1	0.9763
jostle, carousel, and embrace	0.3320	0.8582	0.7868
nest building, jostle, carousel, and embrace	0.1019	0.2796	0.1923
Only reproductive behaviors			
nest building	0.0009v	0.3555	0.0174v
jostle	0.6961	0.1299	0.00004^
carousel	0.8387	0.7970	1
embrace	0.8466	0.9467	0.9144
jostle, carousel, and embrace and Embrace	0.7598	0.4972	0.0467^

* Indicates the first summer was higher.

^ Indicates flow treatment increased.

v Indicates flow treatment decreased.

Table 6. Summary of the significant relationships found in male Neosho madtoms using sequential analysis (alpha = 0.0008). The 'Given' behavior is the first in the sequence with the 'Target' behavior either 1-3 steps (lags) after (n = 18).

		Non-flow			Flow		
Male		Lag			Lag		
Given	Target	1	2	3	1	2	3
nest building	nest building	NA	+	+	NA	+	+
nest building	jostle						
nest building	carousel						
nest building	embrace				- *		
jostle	nest building	+			+		
carousel	nest building						
embrace	nest building						
jostle	jostle	NA	+	+	NA	+	+
jostle	carousel	+		+	+		+
jostle	embrace	+	+	+	*	+	*
carousel	jostle	+	+	+	+	+	+
carousel	carousel	NA	+	+	NA	+	+
carousel	embrace	+		+	+		+
embrace	jostle	+	+	+	+	*	+
embrace	carousel	+	+	+	+	+	+
embrace	embrace	NA	+	+	NA	+	+

\+ Indicates the behavior occurred more than expected.

\- Indicates the behavior occurred less than expected.

NA Indicates that combination was not possible, behaviors could not repeat.

* Indicates differences between treatments.

Table 7. Summary of the significant relationships found in female Neosho madtoms using sequential analysis (alpha = 0.0008). The 'Given' behavior is the first in the sequence with the 'Target' behavior either 1-3 steps (lags) after (n = 18).

		Non-flow			Flow		
Female		Lag			Lag		
Given	Target	1	2	3	1	2	3
nest building	nest building	NA	+	+	NA	+	+
nest building	jostle						
nest building	carousel						
nest building	embrace				**		
jostle	nest building	**			**		
carousel	nest building						
embrace	nest building						
jostle	jostle	NA	+	+	NA	+	+
jostle	carousel	+		+	+		+
jostle	embrace	+	+	+	*	+	*
carousel	jostle	+	+	+	+	+	+
carousel	carousel	NA	+	+	NA	+	+
carousel	embrace	+		+	+		+
embrace	jostle	+	+	+	+	*	+
embrace	carousel	+	+	+	+	+	+
embrace	embrace	NA	+	+	NA	+	+

\+ Indicates the behavior occurred more than expected.

NA Indicates that combination was not possible, behaviors could not repeat.

* Indicates differences between treatments.

** Indicates differences from the male results.

Table 8. Summary of the permutation tests for autocorrelation. The p-values are from a permutation version of the Durbin Watson test. The number of observations and aquaria correspond to the number of tanks that had five or more continuous weeks of collected data. Bonferroni corrected alpha level, 0.05/4 = 0.0125

Summer	Treatment	# observations/ # aquaria	Response Variable	p-value
1	Flow	27/4	hout length	0.9723
			frequency	0.9449
			proportion of time	0.9188
1	Nonflow	27/4	bout length	0.3682
			frequency	0.0695
			proportion of time	0.0971
2	Flow	6/1	bout length	0.2167
			frequency	0.0222
			proportion of time	0.0444
2	Nonflow	18/3	bout length	0.8292
			frequency	0.8002
			proportion of time	0.8272

Table 9. Summary of patterns over time for all reproductive behaviors (combination of nest building, jostle, carousel, embrace) and the three parameters (bout length, frequency, and the proportion of time). The three types of patterns tested were linear, quadratic, and cubic. The corresponding p-values and least absolute deviation regression coefficient of determination (r^1) are given at the bonferroni corrected alpha level 0.05/12 = 0.0042.

				Model type					
		# observations/		Linear		Quadratic		Cubic	
Summer	Treatment	# aquaria	Response variable	p	r^1	p	r^1	p	r^1
1	Flow	38/6	bout length	0.3342	0.0192	0.2918	0.0402	0.7386	0.0426
			frequency	0.4054	0.0321	0.1854	0.0641	0.6478	0.0688
			proportion of time	0.8374	0.0012	0.1030	0.0545	0.9514	0.0546
1	Nonflow	39/6	bout length	0.1124	0.0373	0.0080	0.1694	0.6266	0.1740
			frequency	0.001*	0.0809	0.0004*	0.2414	0.0056	0.3005
			proportion of time	0.0078	0.0458	0.0008*	0.1967	0.0122	0.2495
2	Flow	16/3	bout length	0.4200	0.0535	0.6546	0.0714	0.6968	0.0830
			frequency	0.6852	0.0440	0.7524	0.0550	0.6116	0.0743
			proportion of time	0.4520	0.0478	0.8328	0.0512	0.5560	0.0675
2	Nonflow	18/3	bout length	0.1976	0.0969	0.4752	0.1182	0.6838	0.1330
			frequency	0.0998	0.1129	0.9836	0.1129	0.3556	0.1508
			proportion of time	0.1092	0.0903	0.9862	0.0903	0.4460	0.1168

* Indicates significant at the 0.0042 level.

APPENDIX
FIGURES

Figure 1. Neosho madtom (*Noturus placidus*).

Figure 2. Neosho madtom distribution. The Neosho River basin located in Kansas, Missouri, and Oklahoma contains four large dams and 16 low-head dams (not shown). The Neosho madtom is only found in the mainstem sections of the Cottonwood, Neosho and the Spring rivers (modified from Wildhaber et al. 1999).

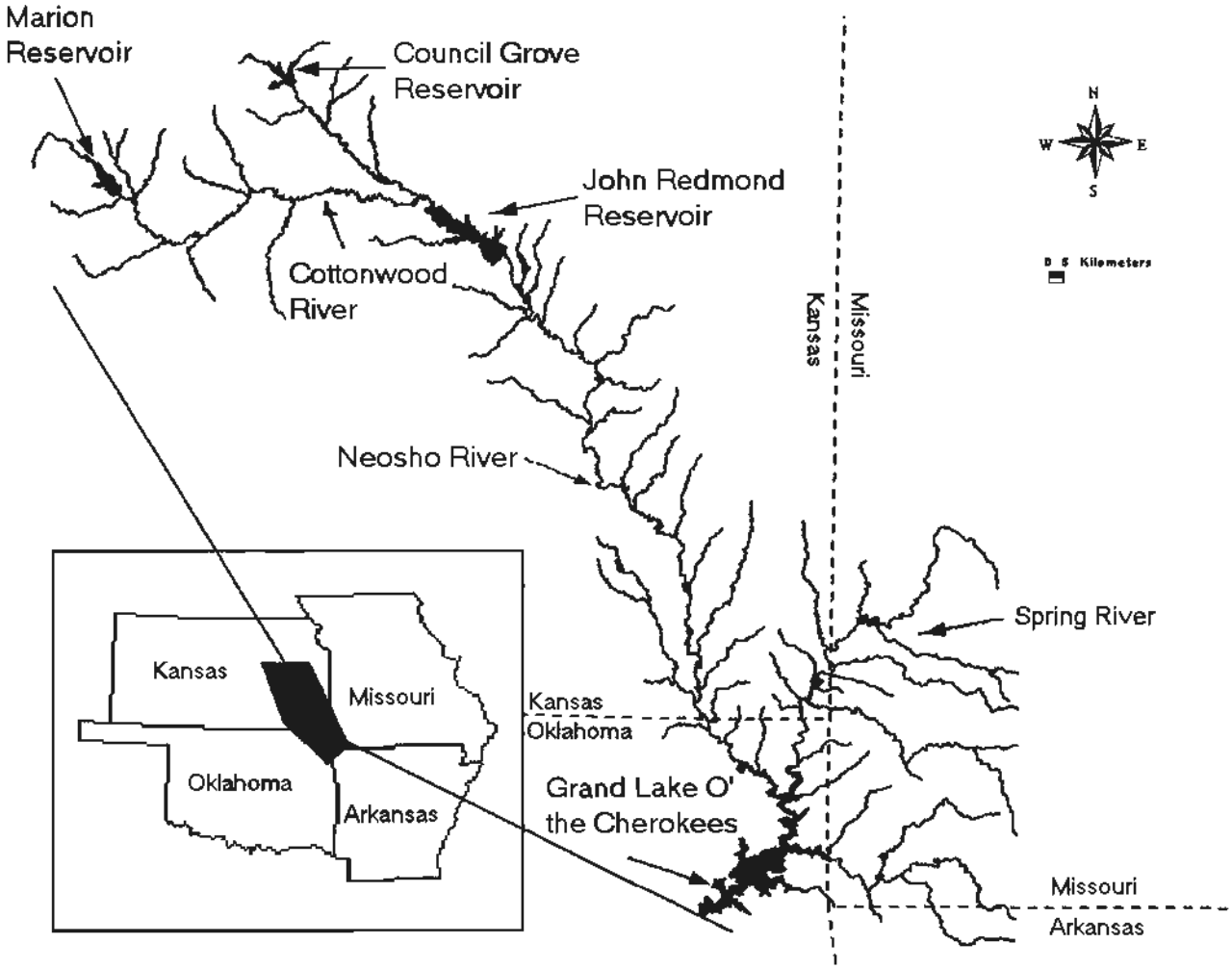

Figure 3. Experiment tank setup showing nest site and recirculating apparatus. This tank was from the second summer of the experiment. 1 = water intake pipe, 2 = water outflow pipe, 3 = heater, 4 = cavity where top-view camera is suspended, and 5 = nesting cavity.

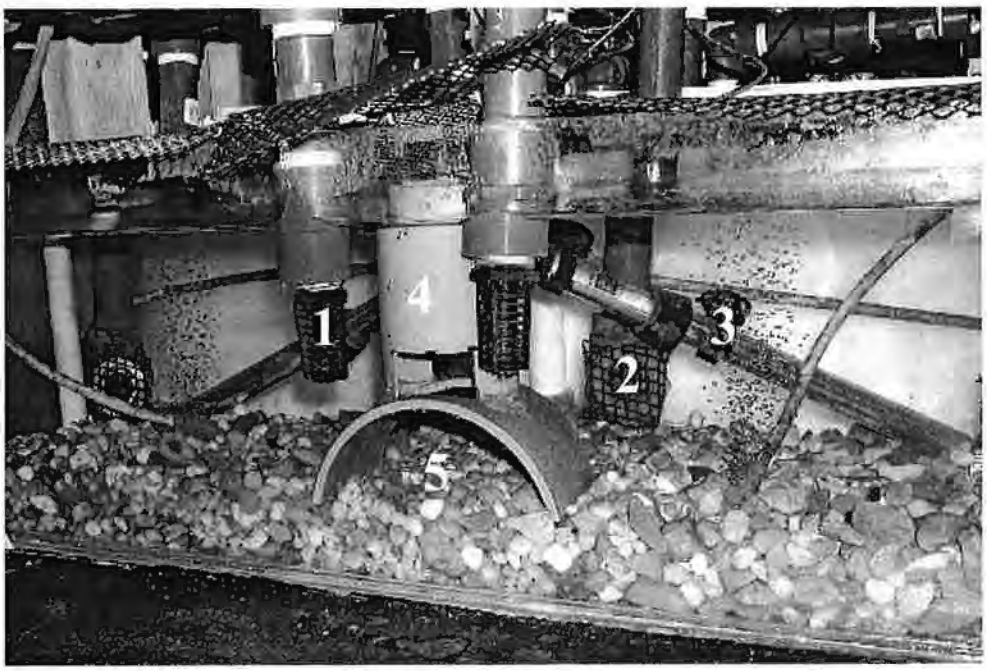

Figure 4. View of the aquarium from the side where a camera was located during the experiment. The two fish are located in the nest.

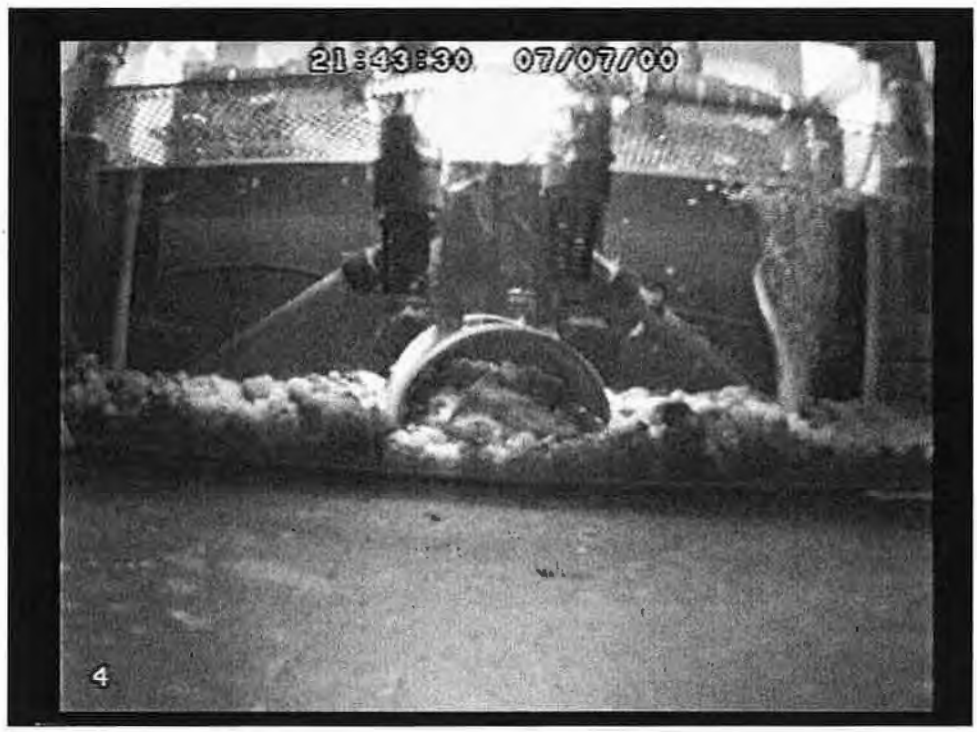

Figure 5. A male Neosho madtom engaged in nest building behavior. He is nudging a rock with his head. The arrow is identifying the male's head and rock.

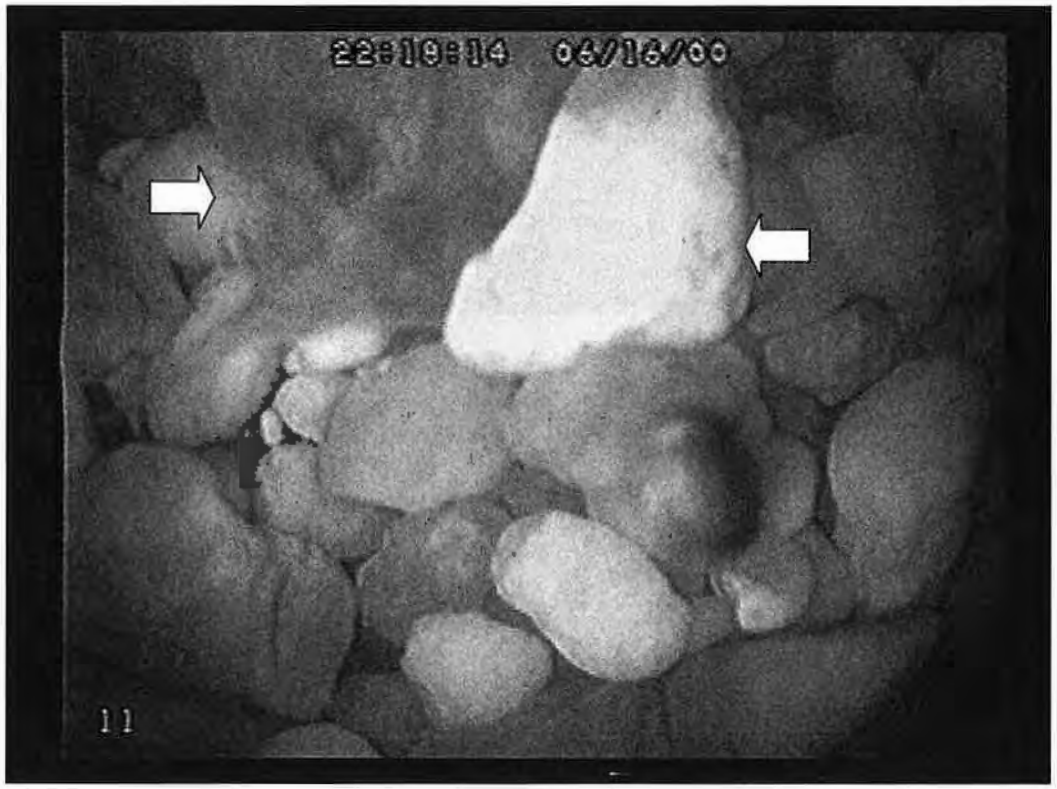

Figure 6. A pair of fish engaged in the jostle behavior. Here the fish swim side to side and up and down but stay in contact with one another. In this picture, female is in the top right corner, male is in the center of the picture. Both fish are facing the right.

Figure 7. A pair of fish engaged in the carousel behavior. The male (bottom) and female (top) nudge each other in the caudal peduncle area and swim in a circular pattern, in this case clockwise. The male is distinguished by the enlarged head and slim abdomen while the female has a smaller head and enlarged abdomen.

Figure 8. A pair of fish engaged in the embrace behavior. Here the male has his fin wrapped around the females head. The male is distinguished by the enlarged head and slim abdomen while the female has a smaller head and enlarged abdomen.
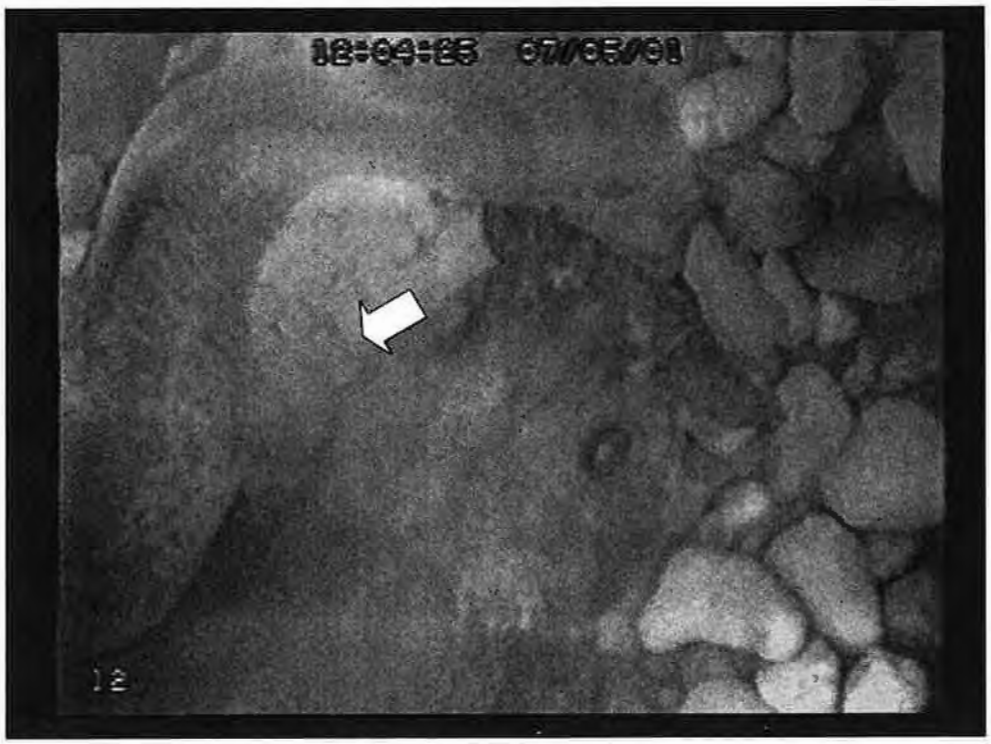
Figure 9. Neosho madtoms spawning. The female is releasing eggs (left, arrow) and male is on the right and has her in an embrace (right).