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Author(s): Geffery R. Luttrell, Anthony A. Echelle, William L. Fisher and David J. Eisenhour

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Declining Status of Two Species of the *Macrhybopsis aestivalis* Complex (Teleostei: Cyprinidae) in the Arkansas River Basin and Related Effects of Reservoirs as Barriers to Dispersal

GEFFERY R. LUTTRELL, ANTHONY A. ECHELLE, WILLIAM L. FISHER, AND DAVID J. EISENHOUR

From 1991 to 1997, we made 323 seine collections at 187 sites to determine the distributional status of two species of the *Macrhybopsis aestivalis* complex, *M. tetranema* (Gilbert) and *M. hyostoma* (Gilbert), in the Arkansas River Basin. A total of 545 *M. hyostoma* and 112 *M. tetranema* were taken in 39 collecting visits to 30 sites. Our survey indicated that the endemic *M. tetranema* has been extirpated from about 90% of its historic range, whereas the more widespread *M. hyostoma* has been extirpated from about 55% of its former range in the basin. Approximate year of extirpation for six populations of *M. hyostoma* in major stream segments was significantly correlated with year-of-completion for reservoirs that would have prevented recolonization from existing populations. This is consistent with the hypothesis that extirpations resulted from disruption of previously existing source/sink relationships among populations. No such correlation was detected for extirpations of seven populations of *M. tetranema*. This result would be expected from the metapopulation model in which the now-extirpated populations of *M. tetranema* were self-sustaining except during unusually harsh conditions (e.g., droughts). This factor apparently explains recolonization of the Cimarron River by *M. hyostoma* subsequent to extirpation of both species of *Macrhybopsis* from this river. The recolonization was delayed by about 25 years, apparently because of reservoir habitat between the Cimarron River and the other major stream draining into the reservoir, the upper Arkansas River, where there was a persistent population of the species.

UNTIL recently, speckled chubs in the Arkansas River Basin and elsewhere (Wallace, 1980) were treated as a single, wide-ranging, geographically variable species, *Macrhybopsis aestivalis*. A recent analysis of *M. aestivalis* from west of the Mississippi River resulted in recognition of two species in the Arkansas River Basin (Eisenhour, 1997, 1999), *M. tetranema* (Gilbert), endemic to the basin, and *M. hyostoma* (Gilbert), a more wide-ranging species. Historically, *M. tetranema* occurred in upstream reaches of the Arkansas River and its larger western tributaries, whereas *M. hyostoma* occupied the middle and lower reaches of the Arkansas River mainstem and its western tributaries. The two species occurred syntopically in southern Kansas and north-central Oklahoma (Eisenhour, 1997).

The impetus for the work described herein was the imperiled conservation status (Cross and Moss, 1987; Williams et al., 1989; U. S. Department of Interior, 1994) of the previously recognized Arkansas River speckled chub *Macrhybopsis aestivalis tetranema* (Gilbert), which included both *M. tetranema* and the Arkansas River population of *M. hyostoma*. Declines in abundance and distribution have also been reported for other fishes (Cross and Moss, 1987; Larson,

1991; Echelle et al., 1995) and bivalve mollusks (Distler and Bleam, 1995) in large portions of the Arkansas River Basin.

Declines of native fishes in southern plains streams have been linked to reservoirs and groundwater removal for irrigation. In the Arkansas River Basin, these activities changed base streamflow levels, altered the periodicity and intensity of flooding over large portions of the drainage, and resulted in periodic or annual summertime dewatering of some upstream reaches (Cross and Moss, 1987; Wahl and Wahl, 1988; Larson, 1991). Such changes alter substrate composition, sediment movement, and channel morphometry (McLaughlin, 1947; Schumm, 1960; Williams and Wolman, 1984). The Arkansas River and its western tributaries are characteristic plains-stream ecosystems (Matthews and Hill, 1980; Matthews, 1988) having wide, shallow, and unshaded channels with sand and gravel substrata and widely fluctuating water levels, turbidity, temperature, and salinity.

Members of the *M. aestivalis* complex, and other declining Arkansas River cyprinids (Moore, 1944; Bottrell et al., 1964; Platania and Altenbach, 1998) spawn semibuoyant eggs during flood conditions. The eggs develop as they

drift, and the larvae continue to drift after hatching. Although not documented, later life stages presumably disperse upstream. Local populations of short-lived cyprinids with this life history are particularly susceptible to extirpation as a result of drought, changes in flow regime, and instream barriers to movement.

For plains-stream fishes, the natural extinction/recolonization dynamic of the metapopulation model (Levins, 1970) and/or immigration in the source-sink model (Pulliam, 1988) may be particularly important in the long-term persistence of many local populations. Plains-stream fishes are often exposed to suboptimal conditions and localized extirpations in their harsh and unpredictable environments. Reservoirs block recolonization, separate population sources from sinks, and prevent movement into refugia during harsh conditions (Bestgen and Platania, 1991; Schlosser, 1995). Consequently, reservoirs as barriers to dispersal appear critical in the decline of stream fishes (Sheldon, 1988; Bestgen and Platania, 1990, 1991). Winston et al. (1991) attributed local extirpation of a form of the *M. aestivalis* complex and three other cyprinids in a portion of the Red River Basin in Oklahoma to a reservoir that prevented recolonization from downstream. The importance of dispersal to persistence in the harsh environments of plains streams is accentuated by anthropogenic changes and associated declines in habitat quality and resulting increased rates of local extirpation. In this paper, we examine the role of reservoirs in the decline of *M. tetranema* and *M. hyostoma* in the Arkansas River Basin.

MATERIALS AND METHODS

The historical distributions of *M. tetranema* and *M. hyostoma* in the Arkansas River Basin were determined by examination of museum specimens listed by Luttrell (1997) and Eisenhour (1997, 1999). We made 323 visits to 187 sites in 1991–1997 to assess the present distribution of the *M. aestivalis* complex in the Arkansas River Basin (Appendix). Detailed collection data and drainage-by-drainage history of collections from the basin are presented by Luttrell (1997). The present distributions of the two species are based primarily on our collections and, to a lesser extent, on museum records of collections by other workers during 1991–1997. Our collections were made with nylon seines either 3.6 or 7.6 m in length (1.8-m deep, 3.2-mm mesh). We attempted to locate and sample all historical collection localities and adjacent stream reaches that appeared to contain suitable habitat (e.g., not inundated by

reservoirs). The collecting protocol evolved from sampling all available habitats (e.g., pools, runs, and backwaters) to concentrating on areas of the main channel with the pea-sized gravel substrata typically occupied by members of the speckled chub complex. The two target species were fixed in 10% formalin, stored in 45% isopropanol, and deposited in the Oklahoma State University Collection of Vertebrates (OSUS). Museum abbreviations used herein follow Leviton et al. (1985) and Poss and Collette (1995).

To assess effects of reservoirs, we compared their cumulative number through time with the cumulative number of extirpations of *M. hyostoma* and *M. tetranema* from different stream reaches. Year-of-completion for reservoirs was taken from Moody et al. (1985). To approximate time of extirpation, we used the last recorded collection of the species from a stream segment. We also computed Pearson product-moment correlations between year of extirpation from a segment of the drainage and year of completion for the reservoir separating the extirpated population from an adjacent area with an extant population.

RESULTS

Distributions.—In our survey of 187 sites in the Arkansas River Basin, we collected 112 *M. tetranema* from four sites and 545 *M. hyostoma* from 26 sites (Fig. 1; Appendix). The results indicate that the Arkansas River Basin endemic *M. tetranema* has disappeared from about 90% of its former range. The species was historically widespread in western reaches of the basin from central Oklahoma westward to Colorado and New Mexico (Eisenhour, 1997; Fig. 1) but now persists only in two widely disjunct areas: (1) the Ninnescah River and an associated portion of the Arkansas River mainstem in Kansas, and (2) the South Canadian River between Ute Reservoir in New Mexico and Meredith Reservoir in the Texas Panhandle.

Macrhybopsis hyostoma has disappeared from about 55% of its historic range in the Arkansas River Basin. The species originally occupied the mainstem of the Arkansas River from Kansas to central Arkansas and downstream reaches of major tributaries (Fig. 1). The present distribution primarily comprises three stream reaches: (1) the mainstem of the Arkansas River between Kaw and Keystone reservoirs and a tributary, the Salt Fork of the Arkansas River downstream of Great Salt Plains Reservoir; (2) an approximately 265 river-km stretch of the Cimarron River downstream from near Keystone Reservoir, and (3) the mainstem Arkansas River

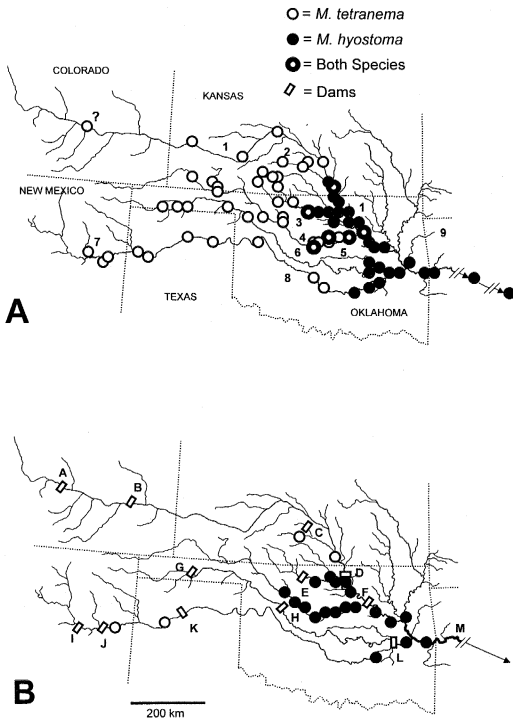


Fig. 1. Historical (A; 1884–1990) and present (B; 1991–1996) distribution of the *Macrhybopsis aestivalis* complex in the Arkansas River Basin. The arrows represent a 400-km downstream segment of the Arkansas River that once supported *M. hyostoma* (see text). Map A: Question mark signifies that the record is assumed to have been *M. tetranema*; 1 = Arkansas River, 2 = Ninescah River, 3 = Salt Fork of the Arkansas River, 4 = Cimarron River, 5 = Deep Fork River, 6 = North Canadian River, 7 = Ute Creek, 8 = South Canadian River, and 9 = Illinois River. Map B: letters represent the following reservoirs: A = Pueblo, B = John Martin, C = Cheney, D = Kaw, E = Great Salt Plains, F = Keystone, G = Optima, H = Canton, I = Conchas, J = Ute, K = Meredith, L = Eufaula; the lower reach of the Arkansas River (M) is the McClellan-Kerr Navigation System. The one locality for *M. hyostoma* upstream of Eufaula Reservoir (L, map B) is based on one specimen taken in 1992 and one in 1994; these probably represent transient, anthropogenic introductions (Luttrell, 1997).

from Keystone Reservoir downstream to near the Oklahoma/Arkansas border.

Macrhybopsis hyostoma apparently has been extirpated from the lower mainstem of the Arkansas River in Arkansas, a 400-km reach of river where the species was locally abundant in the 1880s (Robison and Buchanan, 1988). This reach was greatly modified by the McClellan-Kerr Navigation System, a complex of locks and dams for barge traffic that extends from central Oklahoma to the Mississippi River. Loss of the

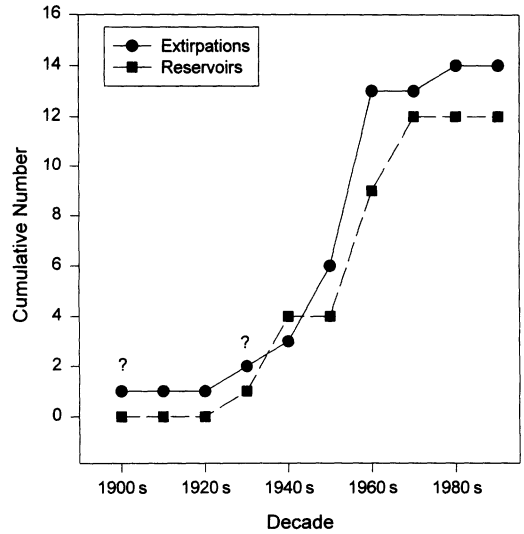


Fig. 2. Cumulative relationship between extirpations of *Macrhybopsis tetranema* and *Macrhybopsis hyostoma* from stream reaches in the Arkansas River Basin upstream of the Oklahoma/Arkansas boundary and completion of the 12 large, flood-control reservoirs (Fig. 1) within the area. Extirpation dates are based on last recorded occurrence. Question marks represent particularly questionable times of extirpation because of infrequent historic sampling in the past; the extirpations in question (*M. tetranema* from the Arkansas River in Colorado and Ute Creek in the South Canadian River drainage of New Mexico) might have occurred considerably later than indicated.

last population of *M. hyostoma* from the river in Arkansas probably coincided with the 1969 completion of Ozark Lock and Dam, which inundated flowing-water habitat in the vicinity of Dardanelle, Pope County (T. Buchanan, pers. comm.). Collections taken in 1993 and 1995 demonstrated persistence of this species in upstream reaches of the McClellan-Kerr Navigation System in Oklahoma (OSUS 26769, 26770) and in the Canadian (OSUS 26360) and Illinois (OSUS 27508) rivers, two major tributaries to the navigation system.

Extirpations and artificial impoundments.—Since 1939, 12 flood-control reservoirs (Fig. 1) and 17 lock and dam structures (McClellan-Kerr Navigation System) have been constructed on streams associated with the historic range of the *M. aestivalis* complex in the Arkansas River Basin (Moody et al., 1985). The period of extirpations (1940s through the 1970s) approximated the period of reservoir construction (Fig. 2).

The correlation between approximate year of extirpation from segments of the Arkansas River Basin with year-of-completion for reservoirs (Ta-

TABLE 1. LAST RECORD OF EXTIRPATED POPULATIONS OF *Macrhybopsis tetranema*, AND THE YEAR-OF-COMPLETION FOR RESERVOIRS THAT ISOLATED AREAS OF EXTIRPATION FROM A SOURCE OF IMMIGRANTS.

Species/Stream segment	Year of last record (Museum No.)	Associated reservoir	Year of completion
1. Arkansas River, Colorado	1889 ^a	John Martin	1948
2. Ute Creek, New Mexico	1939 (MSB 1434)	Ute	1963
3. North Canadian River upstream of Canton Reservoir, Oklahoma	1949 (OSUS 4124) ^b	Canton	1948
4. Arkansas River upstream of Wichita, Kansas	1958 (KU 3938)	Loss of habitat ^c	—
5. S. Canadian River downstream of Meredith Reservoir, Texas	1959 (TU 20140)	Meredith	1965
6. Arkansas River between Kaw and Keystone reservoirs, Oklahoma	1960 (UOMZ 39032)	Kaw	1976
7. Salt Fork of Arkansas River upstream of Great Salt Plains Reservoir, Kansas and Oklahoma	1964 (KU 8574)	Great Salt Plains	1941
8. Cimarron River, Kansas and Oklahoma	1965 (UOMZ 33985)	Keystone	1964

^a Record from Jordan (1891); status of specimens unknown.

^b Collection of a single specimen in 1982 (OSUS 19235), 34 years after the previous collection, probably represents a transient anthropogenic introduction, possibly by the bait industry.

^c Stream-bed dewatered much of the year by ground- and surface-water usage for irrigation (Larson, 1991); not included in the correlation analysis examining effects of reservoirs as barriers to dispersal (see text).

bles 1–2) preventing recolonization from an existing population was significant for *M. hyostoma* (Pearson's product-moment correlation, $n = 6$, $r = 0.89$, $P = 0.02$), but not for *M. tetranema*. The correlation for *M. tetranema* was not significant, regardless of whether two extirpations from poorly sampled areas (Ute Creek, New Mexico and Arkansas River, Colorado) were excluded ($n = 5$, $r = 0.21$, $P = 0.73$) or retained in the analysis ($n = 7$, $r = 0.30$, $P = 0.51$). The correlation for both species combined was not significant when the two poorly sampled areas were either excluded ($n = 10$, $r = 0.58$, $P = 0.08$) or retained ($n = 12$, $r = 0.53$, $P = 0.08$).

Extirpation and recolonization of Macrhybopsis in the Cimarron River.—Extirpation of both *M. tetranema*

and *M. hyostoma* from the Cimarron River by the early 1970s was followed about 25 years later by reestablishment of a population of *M. hyostoma* (Fig. 3). Historically, *M. tetranema* was more abundant and widespread in the drainage than was *M. hyostoma* (Figs. 1,3). Between 1928 and 1965, *M. tetranema* ($n = 620$) was taken in 29 museum-vouchered collections from mainstem and tributary sites of the Cimarron River. Three of those collections, all from mainstem sites, also contained *M. hyostoma* ($n = 19$). The last record of either species from the drainage between 1965 and 1992 was a mainstem Cimarron River collection that contained five *M. tetranema* and one *M. hyostoma*.

For the time period 1966 to 1992, we located data for more than 400 collections from the Ci-

TABLE 2. LAST RECORD OF EXTIRPATED POPULATIONS OF *Macrhybopsis hyostoma*, AND YEAR-OF-COMPLETION FOR RESERVOIRS THAT ISOLATED AREAS OF EXTIRPATION FROM A SOURCE OF IMMIGRANTS OR IS BELIEVED TO HAVE INUNDATED THE LAST AVAILABLE HABITAT IN THE REACH (OZARK LOCK AND DAM—SEE TEXT).

Species/Stream segment	Year of last record (Museum No.)	Associated reservoir	Year of completion
1. N. Canadian River, Oklahoma	1962 (UOMZ 35090)	Eufaula	1964
2. Deep Fork River, Oklahoma	1962 (UOMZ 36211)	Eufaula	1964
3. Arkansas River, Arkansas	1963 (habitat inundated) (OSUS 7224)	Ozark Lock and Dam	1969
4. S. Canadian River, Oklahoma	1965 ^a (KU 5952)	Eufaula	1964
5. Cimarron River, Oklahoma	1965 ^b (UOMZ 33985)	Keystone	1964
6. Arkansas River, Kansas	1984 (KU 21704)	Kaw	1976

^a Collection of single specimens in two separate collections from the South Canadian River just upstream of Eufaula Reservoir in 1992 and 1994 (U. Pigg, pers. comm.; pers. obs.) probably represent recent anthropogenic introductions.

^b Prior to re-invasion by the species in the early 1990s; see text.

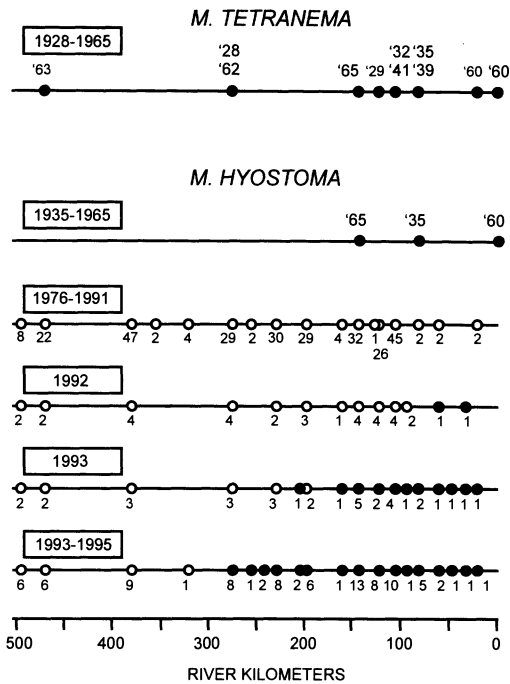


Fig. 3. Changes in occurrence of *Macrhybopsis tetranema* and *Macrhybopsis hyostoma* in the Cimarron River, Oklahoma, mainstem. Open circles = collections not containing either species; black circles = collections containing one or the other of the two species. Numbers above lines = year of collection; numbers below = number of collections.

marron River drainage, none of which contained either *M. tetranema* or *M. hyostoma* (Luttrell, 1997), including 287 collections from the Cimarron River mainstem where the two species, particularly *M. hyostoma*, were most likely to be found. The majority of these collections were made by J. Pigg (1988, unpubl. field notes) in annual surveys, but Marshall (1978), Felley and Cothran (1981), and Larson (1991) also made series of samples from the mainstem. Further, in 1991 and 1992, both species were absent in 17 collections that we made in efforts aimed specifically at locating *Macrhybopsis* in the drainage.

Whether or not the two species of *Macrhybopsis* were absent from the Cimarron River from 1966 to 1992 is problematic because one cannot be certain that a species is present but undetected. The number of site visits (N) needed to conclude with a desired confidence level (α) that a species is absent from an area is given by the equation $N = [\ln(\alpha)] \cdot [\ln(1 - P)]^{-1}$ (Reed, 1996). With 287 visits to Cimarron River mainstem sites from 1966 to 1992 within the historical range, and assuming the chubs were pre-

sent but extremely rare (i.e., $P = 0.05$; five of 100 site visits would produce one or the other of the two species), the probability that they were present at this level, but not detected because of sampling error, is about 4.0×10^{-7} (solving for α). Thus, both *M. tetranema* and *M. hyostoma* apparently were absent from the Cimarron River from 1966 to 1992.

The first post-1965 collections of either *M. tetranema* or *M. hyostoma* from the Cimarron River drainage were collections of *M. hyostoma* by R. Lemmons in September 1992 from two sites on the lower Cimarron River, one near Oilton, Creek Co. (UOMZ 51563; $n = 3$) and one near Cushing, Payne Co. (UOMZ 51562; $n = 1$). Both sites were sampled in 1979 (Felley and Cothran, 1981) and again in 1989 (Larson, 1991) and produced no *M. hyostoma*. In 1992, the species was absent in 32 samples from 11 mainstem sites upstream of Lemmons' localities for the species in that year (J. Pigg, unpubl. field notes; Lemmons et al., as cited in Luttrell, 1997).

In 1993, expansion of the range of *M. hyostoma* was verified by collections of the species ($n = 1-29$) at 10 sampling sites encompassing 190 stream-km of the Cimarron River between Oilton and Dover, Kingfisher Co., Oklahoma. Two sampling sites immediately upstream (30 and 75 km) from Dover, one near Okeene, Kingfisher Co. and one near Cleo Springs, Major Co., failed to produce *Macrhybopsis* in 1993, but single specimens of *M. hyostoma* were taken at both localities in 1994 (J. Pigg, pers. comm), and in 1995 we collected 35 from one of the two sites and 95 from the other. We did not find the species at a site 53 km upstream from Cleo Springs.

DISCUSSION

During the past several decades, the Arkansas River endemic *M. tetranema* and the more widespread *M. hyostoma* have been extirpated from approximately 90% and 55%, respectively, of their historic ranges in the Arkansas River Basin. *Macrhybopsis tetranema* persists only in two widely disjunct areas, the Ninnescah River and an associated portion of the Arkansas River in Kansas (about 100 river-km) and the South Canadian River between Ute and Meredith reservoirs in New Mexico and Texas (about 200 river-km). *Macrhybopsis hyostoma*, which is widespread in the Mississippi River Basin (Eisenhour, 1997), still occupies about 600 river-km that include the Arkansas River mainstem and downstream reaches of major tributaries (Salt Fork, Cimarron, and Canadian Rivers) between Kaw Reser-

voir on the Kansas/Oklahoma border and the Oklahoma/Arkansas border.

The temporal pattern of extirpation for *M. tetranema* and *M. hyostoma* from the Arkansas River Basin coincides well with that for completion of reservoirs. These impoundments contribute in various ways to the decline of native organisms adapted to stream conditions. The most obvious effects are loss of habitat by inundation of streams and dewatering as a result of impoundment and diversion of water out of the streambed. Dewatering is particularly prevalent in western, arid portions of the Arkansas River Basin where once perennial streams now have long periods of no flow or complete dewatering (Wahl and Wahl, 1988). For example, Pueblo and John Martin reservoirs and associated irrigation diversions have contributed to seasonal dewatering of the Arkansas River from the Colorado-Kansas border to near Great Bend (Barton County, Kansas), accounting for the extirpation of *M. tetranema* in this river reach (Cross and Moss, 1987).

A more subtle, less substantiated effect of reservoirs is the potential for increased predation and competition resulting from changes in fish-assemblage structure both upstream and downstream of reservoirs (Echelle and Schnell, 1976; Cross and Moss, 1987). Cross and Moss (1987) suggested that reservoirs contributed to an increased abundance of sight-feeding fishes in plains streams of western Kansas. In the Arkansas River Basin of Oklahoma, the abundance and distribution of inland silverside *Menidia beryllina* increased markedly since it was first taken from the basin in 1964 (Sisk and Stephens, 1964). This expansion agrees with the suggestion (Sisk and Stephens, 1964) that reservoirs favored increased abundance of this species. *Menidia beryllina* is a small, sight-feeding planktivore (Saunders, 1959) that consumes fish eggs (Bettoli et al., 1991). In rivers, *M. beryllina* occurs primarily in the main channel; thus, it may be important in the decline of fishes like *M. tetranema* and *M. hyostoma*, whose eggs and larvae drift in the water column as they develop.

Ultimately, reservoirs are barriers to dispersal and contribute to losses of local populations by blocking postextirpation recolonization. This factor apparently explains the absence of *Macrhybopsis* and three other plains-stream cyprinids from a portion of the Red River Basin in Oklahoma (Winston et al., 1991), and it seems responsible for the 25-year hiatus reported herein for the occurrence of *M. hyostoma* in the Cimarron River. Similarly, Bestgen and Platania (1991) invoked barriers to dispersal to help explain the decline of Rio Grande silvery minnow

Hybognathus amarus in New Mexico and Texas, and Etnier et al. (1979) attributed decline of Mississippi silvery minnow *H. nuchalis* in Tennessee to habitat fragmentation as a result of reservoir construction.

Although extirpations of *M. tetranema* occurred primarily during the period of reservoir construction in Oklahoma, individual extirpations were not closely associated with year-of-completion for reservoirs that would have blocked dispersal from the nearest surviving population. This lack of direct correlation is expected from Levins' (1970) metapopulation model, in which reservoirs would contribute to extirpation by disrupting the extinction/recolonization dynamic among local populations. With this model, date of reservoir completion may be not correspond with date of extirpation because the latter results from other factors. For example, *M. tetranema* persisted in the upper Salt Fork of the Arkansas River for more than 20 years after construction of Great Salt Plains Reservoir and then was extirpated, probably by drought (Luttrell, 1997). Similarly, a population has persisted for more than 30 years between Ute and Meredith reservoirs. This appears to be the largest extant population of *M. tetranema*, possibly because frequent midsummer rains maintain adequate river discharges for reproduction, as suggested for *Notropis girardi* in the area (Bestgen et al., 1989; Larson, 1991).

In contrast with *M. tetranema*, local extirpations of *M. hyostoma* were significantly correlated with year-of-completion for reservoirs blocking recolonization. This correlation is predicted from the hypothesis that extirpations were primarily a result of a disrupted system of source/sink (Pulliam, 1988) populations. With this model, reservoir completion would soon be followed by extirpation of populations dependent on dispersal for their persistence.

Disrupted source/sink dynamics apparently applies to at least three of the six extirpations of *M. hyostoma*. The populations in the North Canadian, South Canadian, and Deep Fork Rivers upstream of the present Eufaula Reservoir probably were historically dependent on dispersal from downstream. The species was historically sparse in these stream reaches (Luttrell, 1997), and analysis of the North and South Canadian rivers suggested that, presently at least, habitats are suboptimal for the species because of a lack of the gravel substrata associated with its occurrence (Luttrell, 1997). Completion of Eufaula Reservoir in 1964 would have separated populations in these areas from those downstream in the Canadian River System where the species still remains. Probably as a

result, the species disappeared upstream of the reservoir between 1962 and 1965.

Conversely, disruption of the metapopulation extinction/recolonization dynamic by Keystone Reservoir apparently explains the history of records for *M. hyostoma* in the Cimarron River. This population disappeared by the early 1970s, reappeared in collections in 1992 and, by 1994, had spread somewhat beyond its historic range in the Cimarron River. Throughout the period of absence, the species persisted in the Arkansas River upstream of Keystone Reservoir. Its failure to recolonize the Cimarron River until the early 1990s probably resulted from unfavorable habitat between the Cimarron and Arkansas river arms of the reservoir. The reappearance of *M. hyostoma* in the Cimarron River may represent transport by humans or natural, although delayed, recolonization from the Arkansas River.

In conclusion, both *M. tetranema* and *M. hyostoma* have declined markedly in the Arkansas River Basin. The direct causes of local extirpation often cannot be assigned with certainty, but water impoundment and diversion projects, drought, and depletions of groundwater are implicated (Cross and Moss, 1987; Wahl and Wahl, 1988; Larson, 1991). Regardless of immediate factors causing local extirpations, the presence of reservoirs and other barriers to recolonization (e.g., dewatered stretches of stream-bed) threaten the two species with continued incremental decline. Both species need continued monitoring, but this is particularly important for *M. tetranema*, which now comprises two widely disjunct, geographically restricted populations. Resource managers should consider repatriating *M. tetranema* in some areas of former occurrence, such as the Cimarron River and the upper Salt Fork of the Arkansas River, where habitat conditions appear suitable for survival (Luttrell, 1997). However, persistent monitoring and repeated repatriation efforts may be required given the harsh nature of the plain-stream environment and the formidable barriers that now fragment the once more continuous range of *M. tetranema*.

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- (GRL, AAE, WLF) U.S. GEOLOGICAL SURVEY, BIOLOGICAL RESOURCES DIVISION, OKLAHOMA COOPERATIVE FISH AND WILDLIFE UNIT, AND DEPARTMENT OF ZOOLOGY, OKLAHOMA STATE UNIVERSITY, STILLWATER, OKLAHOMA 74078; AND (DJE) DEPARTMENT OF BIOLOGICAL AND ENVIRONMENTAL SCIENCES, MOREHEAD STATE UNIVERSITY, MOREHEAD, KENTUCKY 40351. E-mail: (AAE) tony.echelle@okway.okstate.edu. Send reprint request to AAE. Submitted: 21 Oct. 1998. Accepted: 22 March 1999. Section editor: S. A. Schaefer.

APPENDIX. SUMMARY OF SAMPLING IN THIS STUDY (1991–1997) AND HISTORICAL AND PRESENT DISTRIBUTION OF *Macrhybopsis hyostoma* AND *Macrhybopsis tetranema* IN THE ARKANSAS RIVER BASIN. Historical and present status are shown as, respectively, number of pre-1991 and 1991–1997 collections containing the species and (in parentheses) number of specimens; nc = no collections in this study; nr = no known record(s). Locality descriptions and dates for 1991–1997 sampling are given by Luttrell (1997). AR = Arkansas, CO = Colorado, KS = Kansas, NM = New Mexico, OK = Oklahoma, TX = Texas.

Stream: Reach/tributary	Number of sites/ visits (1991–1997)	<i>M. hyostoma</i>		<i>M. tetranema</i>	
		Historical	Present	Historical	Present
Arkansas River:					
John Martin Dam, CO to Wichita, KS	6/6	nr	nr	5 (18)	nr
Wichita, KS to Kaw Reservoir, OK	4/8	4 (15)	nr	7 (38)	3 (17)
Kaw Reservoir to Keystone Reservoir, OK	6/8	22 (351)	4 (151)	1 (1)	nr
Keystone Reservoir to Haskell, OK	3/3	6 (20)	2 (9)	nr	nr
Muskogee, OK to OK/AR border	nc	2 (43)	2 (2)	nr	nr
Small tributaries, OK	1/1	2 (2)	nr	nr	nr
Mainstem in AR	nc	10 (343)	nr	nr	nr
Ninnescah River (KS):					
North Fork Ninnescah River	2/2	nr	nr	2 (120)	nr
South Fork Ninnescah River	5/10	nr	nr	1 (24)	2 (16)
Lower Ninnescah River	2/2	1 (1)	nr	1 (1)	nr
Chikaskia River and tributaries:					
Upstream of Blackwell, OK	33/61	nr	nr	nr	nr
Downstream of Blackwell, OK	6/9	9 (36)	1 (1)	nr	nr
Medicine Lodge River:					
Mainstem in KS	6/19	nr	nr	4 (19)	nr
Mainstem in OK	2/4	nr	nr	nr	nr
Elm Creek, KS	1/1	nr	nr	1 (3)	nr
Salt Fork of the Arkansas River:					
Mainstem in KS	3/3	nr	nr	nr	nr
KS/OK border to great Salt Plains Reservoir	7/14	nr	nr	2 (42)	nr
Downstream of Great Salt Plains Reservoir	11/19	16 (386)	7 (35)	1 (11)	nr
Tributaries in KS	3/5	nr	nr	2 (10)	nr
Tributaries in OK	2/2	nr	nr	1 (3)	nr
Cimarron River:					
Mainstem in KS	2/2	nr	nr	1 (6)	nr
Mainstem in OK	18/39	3 (19)	21 (343)	22 (449)	nr
Crooked Creek (KS)	1/1	nr	nr	3 (13)	nr
Tributaries in OK	26/61	nr	nr	7 (171)	nr
Canadian River:					
The present Lake Eufaula (pre-construction)	nc	3 (56)	nr	nr	nr
Eufaula Dam (OK) to Arkansas River	1/1	3 (23)	1 (10)	nr	nr
Deep Fork River (OK)	6/6	2 (3)	nr	nr	nr
Little Deep Fork River (OK)	1/1	nr	nr	nr	nr
North Canadian River (OK):					
North Canadian River upstream of Harrah	10/11	nr	nr	4 (69)	nr
Harrah to Lake Eufaula	4/4	3 (26)	nr	nr	nr
Western Tributaries (OK)	2/2	nr	nr	2 (24)	nr
South Canadian River:					
Ute Reservoir (NM) to Meredith Reservoir (TX)	2/3	nr	nr	7 (351)	3 (87)
Meredith Reservoir to Lexington, OK	7/10	nr	nr	7 (46)	nr
Lexington, OK to Lake Eufaula	4/5	4 (16)	2 (2)	nr	nr
Revelto Creek in NM	nc	nr	nr	1 (4)	nr
Illinois River (OK):					
	nc	1 (7)	1 (1)	nr	nr