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Habitat and Biology of the Loach Minnow, *Tiaroga cobitis*, in New Mexico

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The eggs of the loach minnow, *Tiaroga cobitis*, were deposited on the undersides of cobble in moderate-velocity riffles. Nearshore larval nursery areas were characterized by slower velocities and smaller substrate particles. Larger individuals occupied higher velocity microhabitats with cobble substrates. Geographic differences in microhabitat distributions of juveniles and adults were minor and were probably related to habitat availability. Male and female *T. cobitis* in their second summer (Age I) comprised the bulk (60%+) of the spawning population. Spawning in the Cliff-Gila Valley reach of the Gila River in New Mexico occurred for a brief period in April 1984 when daytime water temperatures were 16–20 C. Larval growth was rapid, and by autumn, Age-0 fish were 30–35 mm SL. Thereafter, growth was slower and few individuals exceeded 60 mm SL or Age II. *Tiaroga cobitis* fed mainly upon ephemeropteran naiads and chironomid larvae. Destruction and modification of riffle habitat and establishment of nonnative fishes have drastically reduced the range of the species.

THE loach minnow, *Tiaroga cobitis* Girard, once was widespread in low to mid-elevation streams of the Gila River drainage in Arizona, Sonora, and New Mexico (Miller and Winn, 1951; Koster, 1957; Minckley, 1973). However, its range has declined in the past 50–75 yr because of altered flow regimes, destruction of habitat, and introduction of non-native species (Minckley, 1973; Propst et al., 1988). *Tiaroga cobitis* now is found mainly in four comparatively undisturbed streams: Aravaipa Creek and Blue River in Arizona (Minckley, 1973) and portions of the Gila and San Francisco drainages in New Mexico (Koster, 1957; LaBounty and Minckley, 1972; Propst et al., 1988). Although *T. cobitis* is federally protected as a threatened species (Unites States Department of Interior, 1986), its biology is poorly known. Our purpose was to: 1) document the status of *T. cobitis* in New Mexico; 2) describe its life history and microhabitat associations; and 3) identify threats to its continued existence.

STUDY AREA

The study area comprised the warmwater reaches of the Gila and San Francisco river drainages in Catron, Grant, and Hidalgo counties of southwestern New Mexico (Fig. 1) and is described in detail by Propst et al. (1988) and Bestgen and Propst (1989).

Three localities were selected for regular sampling because they represented the array of physicochemical conditions and fish communities normally associated with *T. cobitis*. The sites and their characteristics were as follows.

1) Tularosa River (T6S R18W Sec 33) (Tularosa Site); mean stream width 3 m; predominantly shallow runs separated by short, shallow riffles and pools 0.5–1.2 m deep; substrate, cobble and rubble in riffles, sand and gravel in runs, and sand in pools; mean mid-day water temperature 9.6 C in winter and 24.3 C in summer; riparian vegetation primarily grasses and small willows (*Salix* sp.).

2) West (T12S R14W Sec 26) and Middle (T12S R13W Sec 25) forks of the Gila River (Forks Site); mean stream widths 12 m; runs and riffles common with pools (0.5–2.0 m deep) at bases of large boulders, cliffs, and trees; substrate, cobble to large rubble in riffles, sand to cobble in runs, and sand in pools; mean water temperatures in West and Middle forks, respectively, 9.1 and 10.0 C in winter and 19.7 and 23.8 C in summer; riparian vegetation grasses, forbs, willows, cottonwood (*Populus* sp.), Arizona alder (*Alnus oblongifolia*) and box elder (*Acer negundo*).

3) Gila River between confluence of Mogollon Creek (T14S R16W Sec 31) and Middle Box (T17S R17W Sec 28) with most work near Riverside (T16S R17W Sec 04) (Cliff-Gila Site); stream width 22–45 m; runs common and separated by riffles, pools (0.5–1 m deep) associated with uprooted trees and debris piles; substrate cobble and rubble in riffles, primarily sand else-
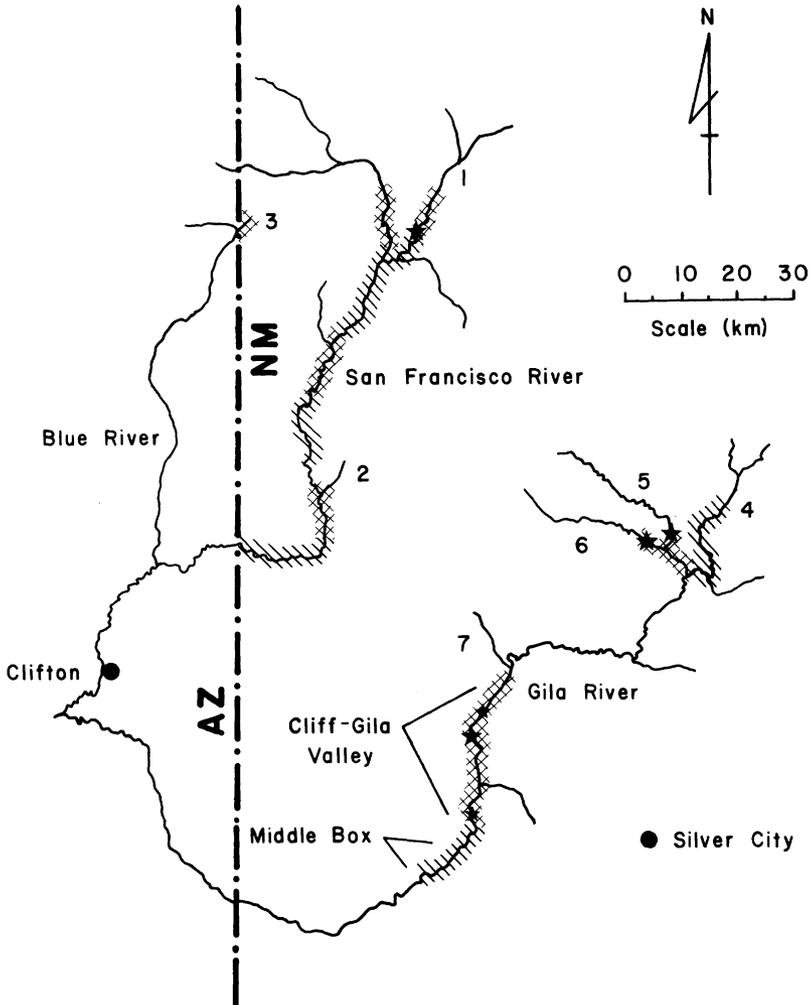
Fig. 1. The Gila-San Francisco River drainage, Arizona and New Mexico. Cross-hatched = reaches of regular occurrence and hatched = reaches of irregular occurrence of *Tiaroga cobitis* in New Mexico. Numerals represent: 1 = Tularosa River, 2 = Whitewater Creek, 3 = Dry Blue Creek, 4 = East Fork Gila River, 5 = Middle Fork Gila River, 6 = West Fork Gila River, and 7 = Mogollon Creek. Large stars = permanent sampling sites; small stars = sites used for estimates of population density.

where; mean mid-day water temperatures 12.8 C in winter, 22.1 C in summer; cottonwoods common in upstream half of valley, Arizona sycamore (*Platanus wrightii*) and willow scattered throughout valley.

METHODS

Habitat.—We obtained elevation and stream gradient information from U.S. Geological Survey 7½' topographic maps. We divided streams into segments in which the topography was fairly homogeneous. Three descriptive categories ("V-canyon," canyon, and valley) provided a reasonable impression of the general features of each segment. The overall pattern in "V-canyon" reaches was a dominance of larger substrates, faster velocity water, and a preponderance of deep run and cascade riffle habitat. Canyon reaches had a more even mix of run, riffle, and pool habitats. In valleys, runs tended to be the most common habitat, substrates were

smaller, and water velocities slower. Stream sinuosity was greatest in valleys and least in V-canyons.

We collected data to describe the microhabitat of juvenile and adult *T. cobitis* at regularly sampled sites on the Tularosa River, West and Middle forks of the Gila River, and Gila River. Data for ontogenetic patterns of microhabitat use were obtained from the Gila River in the Cliff-Gila Valley. Specimens were collected by electrofishing, beginning at the downstream terminus of a site and proceeding upstream in a zigzag pattern. A numbered flag was anchored at each point where *T. cobitis* was collected. We recorded flag number and TL of specimens. Care was taken to avoid frightening fish prior to immobilization. If we suspected our activities influenced fish position, we made no measurements for that observation. Information on ovadeposition sites was obtained by examining randomly selected rocks in riffles occupied by adult *T. cobitis* in the Cliff-Gila Valley. If we found embryos on a rock, counts were made if ≤ 25 and estimated if ≥ 26. Species identity was confirmed by rearing several egg clutches in aquaria.

Following specimen collection at a site, we measured water velocity, water depth, and substrate composition at each microhabitat point. A Marsh-McBirney flowmeter mounted on a topset rod at 0.6 column depth (3.0 cm accuracy) was used to measure water velocity (3.0 cm/sec accuracy). Substrate within a 15 cm radius of a flag was visually characterized as silt (≤ 0.05 mm), sand (0.06–2.0 mm), gravel (2.1–50.0 mm), cobble (51.0–150 mm), rubble (151–300 mm), boulder (>301 mm), or bedrock. Intermediate classifications were used when substrate classes were mixed (e.g., 40% sand–60% gravel = sand-gravel). Thus, a total of 12 coded categories (1 = silt, 2 = silt-sand, 3 = sand, 4 = sand-gravel, 5 = gravel, 6 = gravel-cobble, 7 = cobble, 8 = cobble-rubble, 9 = rubble, 10 = rubble-boulder, 11 = boulder, and 12 = bedrock) were used.

We estimated habitat availability by placing 10 equidistant transects, perpendicular to flow, across the wetted portion of the stream channel. Width of the wetted channel was measured at each transect, and depth, velocity, and substrate measurements were made at 10% of transect-width intervals. Measurements on Tularosa River were made at 30 cm intervals due to small stream width. We used the Kolmogorov-Smirnov (K-S) test (Zar, 1984) to test for significant differences between habitats available and occupied. Significance was interpreted as selection for a subset of the available habitat. Analysis of variance tests (Sokal and Rohlf, 1981) were used to evaluate differences in microhabitat preference between paired life stages and study sites. We pooled microhabitat data (availability and occupied) from the West and Middle forks of the Gila River for analyses.

We arbitrarily divided specimens into developmentally based length-classes (i.e., larva, juvenile, and adult). Specimens 6–19 mm TL were larvae, 20–39 mm TL juveniles, and ≥ 40 mm TL adults.

Distribution and biology.—We examined museum records, published literature, and agency memoranda and reports to characterize the historic distribution and status of *T. cobitis*. To obtain an accurate definition of the current range and status of *T. cobitis*, we sampled almost all lotic, warmwater habitats in the Gila-San Francisco Drainage of New Mexico. Typically, a Smith-Root backpack electrofisher (Type VII-A) with pulsed direct current was used to immobilize fish. Stunned fishes were collected with dipnets or seines and placed in holding pens or preserved for later examination. We also used seines of a variety of lengths (all 3.2 or 6.4 mm mesh) to supplement electrofishing collections. Larval fishes were collected with aquarium dipnets (mesh = 1 mm).

We estimated *T. cobitis* densities in July 1987 at three locations in the Cliff-Gila Valley. Specimens were captured by kick-seining (once) several measured areas in riffles at each site. Depletion sampling (four kick-seine collections/area) was done at one site to evaluate density estimates. Density estimates for each site were an average of all sample efforts within a site. Density estimates probably represent maximal values because they were made during a period of low flow (1.2–1.5 m³/sec) when fish were crowded and Age-0 individuals were common.

All specimens retained were fixed in 10% formalin and preserved in 45% isopropanol or 3% buffered formalin (larvae). Preserved specimens are housed in the New Mexico Department of Game and Fish Laboratory and the University of New Mexico Museum of Southwestern Biology.

Specimens used to characterize the biology of *T. cobitis* were obtained from the Cliff-Gila Valley of the Gila River. Specimens were measured to the nearest 0.1 mm SL and weighed

(after blotting dry) to the nearest 0.1 g. Specimens collected between June 1983 and July 1984 were eviscerated to determine sex, gonadal condition, and diet. We identified all invertebrate food items to family. The ovarian mass removed from each female was blotted dry and weighed (0.01 g accuracy). Ova from a weighed subsample (20–40%) were segregated into maturity modes (maturing, mature, and reproductive; Britt, 1982), counted, and the greatest diameter (nearest 0.01 mm) of at least 10 ova in each mode measured. Maturing ova were white to cream-yellow and <0.90 mm diameter, mature were pale yellow-orange and 0.80–1.80 mm, and reproductive were 1.30–1.80 mm and dark orange. Because there were overlaps in the size ranges of each mode, color was often the key determinant of relative maturity. For each ovary, we determined the total number of ova in each mode by comparing the ratio of ova in each mode in the weighed subsample to the total weight of the ovary. A gonosomatic index (GSI) was calculated by dividing total ovary weight by total body weight and multiplying the result by 100. Use of the GSI as an index of gonadal activity has been questioned and found inappropriate if its assumptions are not met (deVlaming et al., 1982). In the limited manner we used the GSI (indication of time of spawning), most of the problems associated with the index that deVlaming et al. described have been avoided. Regression analysis was used to characterize the relationship between female SL and the number of most-mature mode ova (mature or reproductive) present in the ovary (Feb.–April 1984 specimens). Length-weight relationships (linear regression) for males and females collected in March–April 1984 were calculated and compared by analysis of covariance (ANCOVA) (Sokal and Rohlf, 1981).

We determined the age structure of Cliff-Gila Valley *T. cobitis* for each sample date from length-frequency histograms. Specimens were grouped into 2 mm length-classes for analysis.

RESULTS

Habitat.—The present geographic range of *T. cobitis* in New Mexico is fragmented and the species is uncommon in all but a few stream reaches (Fig. 1). No populations of *T. cobitis* were found above 1980 m elevation, and the specific upper elevation varied among streams, being higher in small streams (i.e., Dry Blue Creek and Tularosa River) than in larger streams (1900 m; i.e., San Francisco River and West and Middle forks of the Gila River).

Gradient, and the implied availability of suitable riffle habitat, also apparently influenced the distribution and abundance of *T. cobitis*. Most large populations of *T. cobitis* occupied stream reaches having a gradient of 3–6 m/km. Notable exceptions were reaches of the Tularosa River and Dry Blue Creek where the gradient was 10.9 and 20.9 m/km, respectively.

The preferred habitat of *T. cobitis* consisted of riffles with substrates ranging in size from sand to rubble, where water velocity ranged from 0–100+ cm/sec, and depths were 6–40 cm. Within riffles, we found that all life stages (embryo, larva, juvenile, and adult) exhibited distinct microhabitat preferences (Table 1). Among the habitat dimensions measured, each life stage of *T. cobitis* occupied subsets of each significantly different from that available, except that no significant difference was found between water velocity occupied by juveniles and that available. Specifically, embryos occurred primarily on large gravel to rubble, in water flowing 30–40 cm/sec, and at depths averaging about 15 cm. Larvae were found in slightly deeper and slower water where substrate particles were smaller. Juveniles inhabited shallower, faster velocity water, with larger substrate particles than that occupied by larvae. Although adults were found over a rather broad range of water velocities, most were found between 24–80 cm/sec. Narrower preferences were noted for depth and substrate; most adults were found associated with gravel to cobble substrate at depths between 12–27 cm.

Geographic comparisons revealed a generally high similarity of microhabitat preferences of juvenile and adult *T. cobitis* among sites (Table 2). Juvenile *T. cobitis* were selective for substrate at all sites and depth and velocity at two of three sites. Between paired sites, no significant differences were found for preferred water velocity and depth, but substrate differences were noted between Tularosa and both Forks and Cliff-Gila.

Adults demonstrated selection for each habitat variable at each location. Among sites, differences in depth of occurrence were not significant. Significant differences in inhabited water velocities were found between Tularosa and Forks and between Tularosa and Cliff-Gila, but not between Forks and Cliff-Gila. The velocities occupied, on average, increased from the smallest stream to the largest. At each lo-

TABLE 1. SUMMARY OF MICROHABITATS OCCUPIED BY *Tiaroga cobitis* EMBRYOS, LARVAE, JUVENILES, AND ADULTS IN THE CLIFF-GILA VALLEY REACH OF THE GILA RIVER, NEW MEXICO. The Kolmogorov-Smirnov Test (K-S) was used to test habitat selection by each life stage and ANOVA (F) was used to evaluate differences in habitat use between paired life stages. Availability data were compiled from 528 velocity-depth-substrate measurements.

| | Available | Occupied | | | |
	Mean ± SD	n	Mean ± SD	K-S[1]	F[1]
		Velocity (cm/sec)			
Embryos	44.0 ± 28.5	79	32.0 ± 20.7	*	
Larvae	44.0 ± 28.5	28	7.3 ± 9.1	*	***
Juveniles	44.0 ± 28.5	37	33.0 ± 23.2	NS	***
Adults	44.0 ± 28.5	95	57.3 ± 21.9	*	***
Embryos	44.0 ± 28.5	79	32.0 ± 20.7		***
		Depth (cm)			
Embryos	29.3 ± 19.2	79	15.5 ± 6.1	*	
Larvae	29.3 ± 19.2	28	16.4 ± 6.7	*	***
Juveniles	29.3 ± 19.2	37	14.9 ± 7.0	*	*
Adults	29.3 ± 19.2	95	18.3 ± 6.7	*	*
Embryos	29.3 ± 19.2	79	15.5 ± 6.1		*
		Substrate (coded)			
Embryos	4.7 ± 1.6	79	6.4 ± 1.3	*	
Larvae	4.7 ± 1.6	29	3.8 ± 1.4	*	***
Juveniles	4.7 ± 1.6	37	5.5 ± 0.9	*	***
Adults	4.7 ± 1.6	95	6.3 ± 1.0	*	***
Embryos	4.7 ± 1.6	79	6.4 ± 1.3		NS

[1] NS = not significant.
 * = <0.05.
 *** = < 0.001.

cation, adults were usually associated with larger substrate particles (gravel-cobble to boulder).

Abundance.—Within stream reaches where *T. cobitis* persists, population densities varied depending upon the quality of riffle habitat. The species was rare or absent where fine sediments filled interstitial spaces. Even where densities were highest (e.g., Cliff-Gila Valley), *T. cobitis* was relatively scarce and almost always the least common native species, rarely constituting more than 10% and usually less than 3% of a collection. Estimated densities in optimal Cliff-Gila Valley riffle habitats did not exceed 1.65/m² and usually were less than 0.5/m².

Reproduction.—The ovarian mass of female *T. cobitis* was easily detected in Age-0 and -I specimens in Sept. 1983, and gradually increased in size through mid-March, when mean GSI was 10.2 and 16.9 for, respectively, Age-I and -II females (Fig. 2). Until Feb., ova were unimodal in size, but two size-classes were obvious in females obtained in March. Ova in the larger size-class were pale yellow-orange and corresponded to the maturing mode. In April, Age I and II mean GSI (17.84 and 26.90, respectively) and reproductive-mode ova diameter (1.38 and 1.53, respectively) peaked. Male gonadal development was less obvious than that of females, but followed a similar pattern of gradual increase through March and peaked in April (mean GSI = 1.55 Age I and 2.77 Age II). After April, female GSI diminished rapidly and by June mean Age-I and -II GSI were 2.80 and 3.60, respectively.

Based upon these data, most *T. cobitis* spawning in the Cliff-Gila Valley occurred over a 4 wk period when daytime water temperatures were 16–20 C. During the spawning period, diel temperature fluctuations ranged from 9–15 C. Age-I females may spawn smaller-sized ova and were less fecund than Age-II females. Age-II *T. cobitis* averaged 159 and 297 reproductive-mode ova on 4 and 13 April, respectively, whereas Age-I females averaged 142 and 145 ova on the same dates. A length-fecundity (most-mature mode) relationship of n = −236.79 + 8.94SL

TABLE 2. SUMMARY OF MICROHABITATS OCCUPIED BY *Tiaroga cobitis* JUVENILES AND ADULTS IN THE GILA-SAN FRANCISCO DRAINAGE, NEW MEXICO. The Kolmogorov-Smirnov test (K-S) was used to evaluate microhabitat selection at each site and ANOVA (F) was used to characterize differences in microhabitat use between paired sites. Availability data were compiled from 210, 870, and 528 velocity-depth-substrate measurements made at Tularosa, Forks, and Cliff-Gila study sites, respectively.

						Occupied				
	Available		Juveniles				Adults			
Site	Mean ± SD	n	Mean ± SD	K-S[1]	F[1]		n	Mean ± SD	K-S	F
				Velocity (cm/sec)						
Tularosa	22.3 ± 15.9	12	29.9 ± 18.3	NS			103	39.6 ± 22.3	*	
Forks	31.1 ± 26.0	63	32.4 ± 16.5	*	NS		58	52.7 ± 19.5	*	***
Cliff-Gila	44.0 ± 28.5	37	33.2 ± 23.2	*	NS		95	57.3 ± 21.9	*	NS
Tularosa	22.3 ± 15.9	12	29.9 ± 18.3		NS		103	39.6 ± 22.3		***
				Depth (cm)						
Tularosa	15.8 ± 8.9	12	16.0 ± 3.4	NS			103	18.0 ± 6.4	*	
Forks	23.1 ± 17.1	63	18.0 ± 9.8	*	NS		58	17.4 ± 5.8	*	NS
Cliff-Gila	29.3 ± 19.2	37	14.9 ± 7.0	*	NS		95	18.3 ± 6.7	*	NS
Tularosa	15.8 ± 8.9	12	15.8 ± 3.4		NS		103	18.0 ± 6.4		NS
				Substrate (coded)						
Tularosa	5.0 ± 2.5	12	7.6 ± 1.0	*			103	7.2 ± 1.6	*	
Forks	5.4 ± 2.1	63	6.0 ± 2.0	*	*		58	6.9 ± 1.3	*	NS
Cliff-Gila	4.7 ± 1.6	37	5.5 ± 0.9	*	NS		95	6.3 ± 1.0	*	**
Tularosa	5.0 ± 2.5	12	7.6 ± 1.0		***		103	7.2 ± 1.6		***

[1] NS = not significant.
 * = <0.05.
 ** = <0.01.
 *** = <0.001.

was calculated (r² = 0.66) (age-classes combined) for Feb.–April (n = 37).

The sex ratio of the 1983 year-class was 1:4.17, male to female, while that of the 1982 year-class was 1:1.09 (Sept. 1983–July 1984). The skewed sex ratio of the 1983 year-class was probably not a sampling artifact because females of the 1983 year-class outnumbered males by a large margin on all, except one, sampling dates and no a priori selection of specimens for examination was made. Although we found no evidence of late summer or early autumn spawning, spawning by *T. cobitis* was observed in Aravaipa Creek, Arizona on 23 Sept. 1988 (M. E. Douglas, D. A. Hendrickson, and W. L. Minckley, pers. comm.).

Adhesive ova of *T. cobitis* were deposited on the undersurfaces of flattened rocks which were slightly elevated from the stream bottom on the downstream side. These rocks were nearly always fine-grained basalt-type material and had smooth surfaces; coarse-grained stones with pocked or rough surfaces were not used for ova deposition. Embryos were most commonly found on rocks 3–5 × 10–18 cm. Such rocks were in

riffles normally inhabited by adults and interstitial spaces were free of fine sediments. Ova were typically deposited side-by-side in a single layer on the rock surface. The number per rock (n = 79) ranged from 4–250 ($\bar{x}$ = 52). Field estimates of clutch size ranged from 40–100 embryos. Most embryos appeared to be viable (bright orange); however, several clutches in shallow, slow-velocity water (<5 cm/sec) had fungal infections and some embryos were opaque. Poor hatching success and dense fungal growth on embryos reared in laboratory aquaria attested to the importance of flowing water to embryo viability. Naturally fertilized embryos in aquaria (18–20 C) had maximum incubation time of 5 d and averaged 5.4 mm TL at hatching.

Age and growth.—Posthatching growth of *T. cobitis* was rapid through Sept./Oct. The 1984 and 1983 year-classes attained a mean SL of 30 mm by late Aug. and Sept., respectively. *Tiaroga cobitis* grew little in winter. In Dec. 1983, for example, the 1982 and 1983 year-classes averaged 48 and 38 mm SL, respectively, and av-
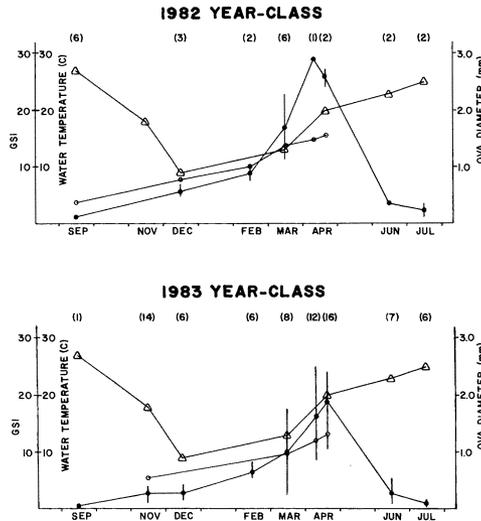
Fig. 2.   The reproductive cycle of *Tiaroga cobitis* from the Cliff-Gila Valley, New Mexico. Open and solid circles = mean ova diameter and mean GSI, respectively; vertical lines = GSI range. Numerals in parentheses = number of specimens examined on each sampling date. Open triangles = water temperature on each sampling date.

eraged only 49 and 37 mm SL in March 1984. After spawning, the 1982 and 1983 year-classes were 5 and 3 mm larger, in average, respectively, than in March. The largest female collected was 56 mm SL (Age II, 13 April 1984) and the largest male was 62 mm SL (Age II or III, 14 March 1984).

Females were significantly larger than males (t = 2.41, $P < 0.05$) in the 1982 year-class, but not in the 1983 year-class (t = 0.72, $P > 0.05$). Male and female length-weight relationships (WT = −5.401 + 0.161SL [n = 13] and WT = −4.081 + 0.135SL [n = 37], respectively) were not significantly different during the spawning season (ANCOVA, F = 1.73, $P > 0.05$).

Population age structure.—Length-frequency analysis (2 mm classes) of Cliff-Gila specimens indicated that this population comprised two to three age-groups throughout the study. Age-0 fishes were common in June 1983 collections, and comprised 50% or more of the population during the remainder of the year. Age-I and -II fishes were 26 and 6%, respectively, of the population during the same period. In 1984, Age-I *T. cobitis* were 66–77% of the population prior to the spawning season, 79% during spawning (April), and only 7% in August. Age-II fish in

1984 had a similar pattern: 23–31% prior to spawning, 21% during spawning, and 1% in Aug. Age-0 *T. cobitis* comprised 63–92% of the population in June–Aug. 1984. Other populations (e.g., Tularosa and Forks) had similar age structures on comparable sampling dates. Based upon these data, maximum longevity of *T. cobitis* is about 36 mo. Most *T. cobitis*, however, do not survive more than 18 mo.

Food habits.—*Tiaroga cobitis* of all life stages were exclusively insectivorous in all seasons. The primary food of larvae and juveniles were chironomid larvae and ephemeropteran naiads (mainly Baetidae). Adults fed largely on these food items, but also consumed Plecoptera, Trichoptera (mainly Hydropsychidae), and Simuliidae. Ephemeropteran naiads were important food items throughout the year for adults, while dipteran larvae were most commonly fed upon in winter months. Ephemeropteran naiads were the most frequent and volumetrically most important dietary items. Although numerically common, dipteran larvae were a small volumetric portion of a stomach's contents. Food habits of *T. cobitis* in the Gila River were not notably different from that reported for the species in Aravaipa Creek (Schreiber and Minckley, 1981).

Associated fish community.—Six native species (*Agosia chrysogaster*, *Gila robusta* and *Meda fulgida* [Gila River only], *Rhinichthys osculus*, *Catostomus insignis*, and *C. clarki*) occurred within the New Mexico range of *T. cobitis*. Collections and underwater observations indicated that *R. osculus* and small (75–150 mm TL) *C. insignis* and *C. clarki* occupied the riffles inhabited by *T. cobitis*. *Catostomus insignis* was found primarily in slower velocity portions of riffles and *C. clarki* and *R. osculus* mainly in faster water with *T. cobitis*. *Rhinichthys osculus* occupied mid-water areas, and *C. clarki* was found around and on larger substrata. The microhabitats of the remaining native species did not or only slightly overlapped that of *T. cobitis* (DLP and KRB unpubl.).

Only three of the 15 non-native species that have been recently documented in the Gila Drainage, New Mexico (Propst et al., 1988) were found in habitats occupied by *T. cobitis*. *Pimephales promelas* and *Gambusia affinis* were sometimes associated with larval *T. cobitis*. *Ictalurus punctatus* was occasionally collected in riffle habitats with adult *T. cobitis*, and remains of the latter were found in *I. punctatus* digestive tracts (D. A. Hendrickson, pers. comm.). Other non-native species were uncommon or occurred mainly in stream reaches not currently occupied by loach minnow.

DISCUSSION

In a region characterized by seasonally unpredictable precipitation, prolonged droughts, and severe floods, conditions would appear adverse for a highly specialized riffle dweller like *T. cobitis*. Seasonal fluctuations in stream discharge alternately inundate and expose riffles, extended periods of depressed flows greatly diminish riffle area, or scouring floods dramatically shift, eliminate, and create riffles. In addition to being subject to loss because of variable flow regimes, riffles suitable for *T. cobitis* occupancy are patchily distributed in streams of the Gila River drainage. Indeed, the variable quality and overall paucity of riffle habitat together with restriction to riffles and apparently low population densities in optimal habitat suggests that *T. cobitis* generally was not abundant historically in its native range.

Tiaroga cobitis persists mainly in streams having relatively natural flow regimes and a predominance of native species. Only two other native species (*R. osculus* and *C. clarki*) regularly inhabit riffles occupied by *T. cobitis* and differ-

ential microhabitat use among them was evident. The foods (mainly ephemeropteran naiads and chironomid larvae) and reduced swim bladder attest to the largely benthic habits of *T. cobitis*. In comparison, *R. osculus* ingests a greater variety of invertebrates (including drift) while *C. clarki* gleans aufwuchs from the substrate (Minckley, 1973; Schrieber and Minckley, 1981; DLP and KRB unpubl.). Thus, these species differ in the use of both microhabitat and spatial resources.

During our study, two major floods occurred in the Gila Basin (U.S. Geological Survey 1982–86), but no appreciable negative impacts were detected in populations of *T. cobitis*. The mechanisms by which *T. cobitis*, as well as other native fishes, avoid entrainment and, thus, displacement by floods are not clearly understood (Meffe, 1984; Minckley and Meffe, 1987; Meffe and Minckley, 1987). We believe that the relative position of *T. cobitis* in riffles is a partial explanation for its resistance to displacement by flood. The narrow velocity and depth preferences of *T. cobitis* over a range of flows generally limit it to portions of riffles intermediate between the shore (slowest velocity) and midstream (fastest velocity). Thus, *T. cobitis* moves from the stream center if flows increase and towards the center if flows decline.

In several aspects of its biology, particularly reproductive, *T. cobitis* demonstrates specializations for survival in riffles of desert streams. *Tiaroga cobitis* males and females are sexually mature by their second spring (Age-I). Although Age-II females contain substantially more reproductive-mode ova than Age I, the younger age-class is always much more numerous than the older. Thus, Age-I females contribute the majority of the ova for a year's reproductive effort. Given the apparently high mortality of older *T. cobitis*, it would be advantageous for an individual to reproduce at a young age. Deposition of ova on the undersurfaces of rocks in moderate-rapid velocity water, usually away from stream margins, ensures that embryos remained in watered riffles and were well-oxygenated.

The benthic and cryptic habits of *T. cobitis* reduce predation risk. The only potential native fish predator is *Gila robusta*; a pool-dweller (Bestgen and Propst, 1989) and therefore not likely to encounter *T. cobitis*.

The foregoing characteristics (early sexual maturity, adhesive embryos, and cryptic behavior) have been documented for small species of

several freshwater fish families (e.g., *Noturus flavus*, Walsh and Burr, 1985; *Etheostoma nigrum*, Winn, 1958; *Cottus hypselurus*, Burr and Warren, 1988) and are not unique to *T. cobitis*. However, among species inhabiting fluvial habitats of the American Southwest, no other species has been documented to have this suite of specializations.

Those characteristics that enable *T. cobitis* to survive the fluctuating harsh environments of desert streams, however, are not sufficient for persistence in human-altered streams. Where flows are diverted, riffles are among the first habitats to be diminished or lost. Water withdrawals cause fragmentation of the range of *T. cobitis*. This pattern is particularly evident in the San Francisco River where diversion for agriculture occasionally dewaters the river in valleys. Recolonization of such areas may occur during periods of sustained flow. If riffle loss is frequent and extensive, however, re-establishment success is correspondingly lowered. Canyon reaches may serve as refugia from which *T. cobitis* re-populates areas subject to habitat degradation. Where natural flooding has been eliminated by stream regulation, riffles are reduced and habitat quality is diminished.

We found little direct evidence of negative effects of non-native fishes upon *T. cobitis*, but the species persists only where the community is dominated by native fishes. Continued domination of native fishes in such areas probably depends upon maintenance of natural flow cycles, particularly floods. Some non-native fishes are differentially displaced and almost eliminated by floods (Minckley and Meffe, 1987; DLP and KRB unpubl.).

The current distribution of *T. cobitis* provides strong evidence for the deleterious effects of human alterations of lotic systems upon the species. Where streams remain unregulated and water withdrawals are not extensive or severe and native fishes dominate communities, *T. cobitis* remains comparatively common. These areas are now limited to Aravaipa Creek and Blue River in Arizona and portions of the Gila-San Francisco Drainage in New Mexico.

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LITERATURE CITED

BARBER, W. E., AND W. L. MINCKLEY. 1966. Fishes of Aravaipa Creek, Graham and Pinal counties, Arizona. Southwest. Natur. 11:313–324.

BESTGEN, K. R., AND D. L. PROPST. 1989. Distribution, status, and notes on the ecology of *Gila robusta* (Cyprinidae), in the Gila River drainage, New Mexico. *Ibid.* 34:402–412.

BRITT, K. D., JR. 1982. The reproductive biology and aspects of life history of *Tiaroga cobitis* in southwestern New Mexico. Unpubl. M.S. thesis, New Mexico State University, Las Cruces, New Mexico.

BURR, B. M., AND M. C. WARREN, JR. 1988. Nests, eggs, and larvae of the Ozark sculpin, *Cottus hypselurus*. Copeia 1988:1089–1092.

deVLAMING, V., G. GROSSMAN AND F. CHAPMAN. 1982. On the use of the gonosomatic index. Comp. Biochem. Physiol. 73A:31–39.

KOSTER, W. J. 1957. Guide to the fishes of New Mexico. University of New Mexico Press, Albuquerque, New Mexico.

LaBOUNTY, J. F., AND W. L. MINCKLEY. 1972. Native fishes of the upper Gila River, New Mexico, p. 134–146. *In:* Symposium on rare and endangered wildlife of the southwestern United States. New Mexico Department of Game and Fish, Santa Fe, New Mexico.

MEFFE, G. K. 1984. Effects of abiotic disturbance on co-existence of predator and prey species. Ecology 65:1525–1534.

———, AND W. L. MINCKLEY. 1987. Persistence and stability of fish and invertebrate assemblages in a repeatedly disturbed Sonoran Desert stream. Amer. Midl. Natur. 117:177–191.

MILLER, R. R., AND W. E. WINN. 1951. Additions to the known fish fauna of Mexico: three species and one subspecies from Sonora, J. Wash. Acad. Sci. 41:83–84.

MINCKLEY, W. L. 1973. Fishes of Arizona. Arizona Game and Fish Department, Phoenix, Arizona.

———, AND G. K. MEFFE. 1987. Differential selection by flooding in stream fish communities of the arid American Southwest, p. 93–104. *In:* Community and evolutionary ecology of North American stream fishes. W. J. Matthews and D. C. Heins (eds.). University of Oklahoma Press, Norman, Oklahoma.

PROPST, D. L., K. R. BESTGEN AND C. W. PAINTER. 1988. Distribution, status, biology, and conserva-

tion of the loach minnow, *Tiaroga cobitis* Girard, in New Mexico. U.S. Fish and Wildlife Service, Endangered Species Report Series 17:1–75.

SCHREIBER, D. C., AND W. L. MINCKLEY. 1981. Feeding interrelationships of native fishes in a Sonoran Desert stream. Great Basin Natur. 41:409–426.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. W. H. Freeman & Company, San Francisco, California.

WALSH, S. J., AND B. M. BURR. 1985. Biology of the stonecat, *Noturus flavus* (Siluriformes: Ictaluridae), in central Illinois and Missouri streams, and comparisons with Great Lakes populations and congeners. Ohio J. Sci. 85:85–86.

WINN, H. E. 1958. Comparative reproductive behavior and ecology of fourteen species of darters (Pisces—Percidae). Ecol. Mongr. 28:155–191.

U.S. DEPARTMENT OF INTERIOR. 1986. Endangered and threatened wildlife and plants; determination of threatened status for the loach minnow; final rule. Federal Register 51:39468–39478.

U.S. GEOLOGICAL SURVEY. 1920–1987. Water-supply records for New Mexico. U.S. Geological Survey, Albuquerque, New Mexico.

ZAR, J. H. 1984. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

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Intra-individual Ploidy Consistency Among Unisexual *Ambystoma*

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Forty unisexual salamanders of the *A. laterale-texanum* complex were examined for ploidy mosaicism using flow cytometry of nuclei derived from erythrocytes, liver, and spleen cells. One triploid-tetraploid mosaic was found, all other specimens were of uniform ploidy, including across tissue types. Thus, mitotic aberrations may be an infrequent feature of populations of unisexual *Ambystoma*. Such phenomena in unisexual vertebrates may be dependent on the relative age of the complex in question. Ploidy constancy observed among tissues validates the practice of comparing results from techniques based on different tissue types.

UNISEXUAL *Ambystoma* of hybrid origin occur from throughout the Great Lakes region to New England and the Maritime Provinces of Canada. Individuals are usually diploid or triploid, but occasionally tetraploid, and are comprised of a variety of genomic complements from *Ambystoma laterale*, *A. jeffersonianum*, *A. texanum*, and *A. tigrinum* (Uzzell and Goldblatt, 1967; Kraus, 1985a; Bogart et al., 1987). Unisexual *Ambystoma* were long presumed to be gynogenetic, based on evidence that nuclei of ova in prophase were routinely hexaploid and, thus, apparently underwent a premeiotic endoduplication (Macgregor and Uzzell, 1964; Cuellar, 1976). But evidence of allozymic variation within egg masses and among the progeny of single females (Bogart, 1982; Bogart and Licht, 1986; Bogart et al., 1987) was inconsistent with this explanation and led to the supposition that they employed, instead, a strictly syngametic reproductive mechanism (Bogart and Licht, 1986; Lowcock et al., 1987; Bogart, 1989). Kraus (1989) pointed out weaknesses in the latter hypothesis and argued that multiple reproductive mechanisms were likely being utilized by these salamanders. This has since been verified by Bogart et al. (1989), who found that unisexual *Ambystoma* reproduce predominantly by gynogenesis at low temperatures, but have an elevated rate of syngamy at higher temperatures. The rate of meiotic reduction events was rather constant with temperature, varying from 13.5%