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Long-term changes in seasonal fish assemblage dynamics in an adventitious desert stream

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LONG-TERM CHANGES IN SEASONAL FISH ASSEMBLAGE DYNAMICS IN AN ADVENTITIOUS DESERT STREAM

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ABSTRACT—Tornillo Creek, a tributary of the Rio Grande in Texas, United States, has historically been an important nursery and spawning habitat for several native fish species. We examined variation in the seasonal fish assemblages in Tornillo Creek within and between two time periods (1967–1970 vs. 2009–2011), and contemporary fish assemblage–environment associations, in order to understand what environmental factors were associated with seasonal fish abundance and occupancy patterns. Our results indicated that fish assemblages were very different between the two time periods. Contemporary seasonal fish assemblage patterns in Tornillo Creek were less variable than historical assemblages and were linked to several environmental factors including water temperature, stream depth, and current velocity. We suggest that the maintenance of stream flow and connectivity are important for the immigration and emigration of certain riverine fishes in Tornillo Creek and that decreases in stream flow could accelerate the domination of the tolerant species in the creek.

RESUMEN—Tornillo Creek, un afluente del río Grande en Texas, Estados Unidos, ha sido históricamente un importante criadero y hábitat de desove para varias especies de peces nativas. Examinamos la variación en los ensamblajes de peces estacionales en Tornillo Creek dentro y entre dos periodos de tiempo (1967–1970 vs. 2009–2011), y las asociaciones del ensamblaje de peces y el ambiente contemporáneo para entender qué factores ambientales se asociaron con los patrones estacionales de presencia y abundancia de peces. Nuestros resultados indican que los ensamblajes de peces fueron muy diferentes entre los dos periodos de tiempo. Patrones de ensamblaje de peces estacionales contemporáneos en Tornillo Creek fueron menos variables que los ensamblajes históricos y estuvieron vinculados a varios factores ambientales como la temperatura del agua, profundidad del arroyo y velocidad de la corriente. Sugerimos que el mantenimiento del flujo y la conectividad son importantes para la inmigración y la emigración de ciertos peces fluviales en Tornillo Creek y que las disminuciones en el flujo de corriente podrían acelerar la dominancia de las especies tolerantes en el arroyo.

River tributaries serve a variety of important ecological roles for fishes in riverine systems. For example, tributaries may serve as feeding, spawning, and nursery habitats for fish taxa (Curry and Spacie, 1984; Gorman, 1986; Schlosser, 1991; Matthews, 1998; Meyer et al., 2007; Corrêa et al., 2011) and can provide less flood-tolerant species with temporal refugia from flood disturbances in the mainstem river channel (Gido et al., 1997; Thornbrugh and Gido, 2010; Koizumi et al., 2013). Fish dispersal and migration between the mainstem and tributaries for spawning, nursery, and refugia can greatly increase the temporal variability in fish assemblages in river tributaries (Schlosser, 1991; Matthews, 1998; Schaefer and Kerfoot, 2004; Meyer et al., 2007; Roberts and Hitt, 2010; Miyazono and Taylor, 2013b). Because adventitious tributaries tend to be maintained by spring flow with clearer and thermally more-stable water than

mainstem river channels (Hubbs and Wauer, 1973), certain fish species might be adapted to their unique habitats. It is important to examine long-term changes in the composition and variability of seasonal fish assemblages in tributaries in order to understand their historical importance to the life histories of fish species in a given river system.

Tornillo Creek, a tributary of the Rio Grande in Texas, United States, has historically been an important nursery and spawning habitat for fishes in the Rio Grande system (Hubbs and Wauer, 1973). Hubbs and Wauer (1973) studied seasonal fish assemblage patterns in Tornillo Creek from 1967 to 1970 and found high variability, suggesting that certain riverine fishes seasonally migrated between the mainstem and the tributary. Furthermore, they suggested that *Fundulus zebrinus*, a nonnative species, might have negatively affected native fish species in the

creek such as *Campostoma ornatum.* We hypothesized that after 40 y this nonnative species, and perhaps others known to exist in the system, might have increased their relative abundance and persistence in the creek and replaced certain native species, leading to distinct changes in the fish fauna across the two time periods and a new "normal" regarding seasonal fish assemblage composition and variability in the creek. To test this hypothesis, we examined long-term changes in seasonal fish assemblages in Tornillo Creek for two time periods separated by approximately 40 y (1967–1970 vs. 2009–2011). We predicted higher seasonal variation for historical assemblages and a strong assemblage shift across time.

We also examined contemporary fish assemblage–environment associations in Tornillo Creek in order to understand what environmental factors were associated with seasonal fish abundance and occupancy patterns. We hypothesized that the seasonal fish assemblages could be modeled by water quality and habitat size. Water quality, including water temperature, can influence the persistence and migration of certain fish taxa in tributaries (Edwards, 1977; Gido et al., 1997). Furthermore, increased stream size can facilitate fish dispersal from the mainstem by increasing the access to the creek (Nunn et al., 2010; Gido and Propst, 2012). Likewise, decreased stream size can decrease the abundance of intolerant species because drying stream pools can have harsh environmental conditions (Capone and Kushlan, 1991; Taylor and Warren, 2001; Love et al., 2008).

MATERIALS AND METHODS—*Study Area and Data Collection*—We conducted seasonal fish collections in Tornillo Creek in November in 2009; in March, August, September, October, November, and December in 2010; and in January, February, March, April, May, June, and July in 2011 (total, 14 samples; Appendix). We sampled fishes with a seine (4.2 m × 1.7 m, 5-mm mesh) for approximately 30 min from the confluence with the Rio Grande, working in an upstream direction approximately 300–350 m (29°10′37.81″N, 103°0′0.50″W). We sampled all available habitat types (i.e., riffles, pools, and runs) within the representative stream reach (Williams et al., 2004). Collected fishes were fixed in 10% formalin and returned to the lab for identification and preservation in 50% ethanol. We curated all fish collections into the Texas Natural History Collection (TNHC). We used historical (1967–1970) seasonal fish assemblage data (total, 11 samples; Appendix) from Hubbs and Wauer (1973) to examine the long-term changes in seasonal fish assemblages in Tornillo Creek.

For each time period, we also collected an array of habitat data. Measured environmental variables included water temperature, dissolved oxygen, specific conductance, mean depth, mean width, and maximum current velocity. We used a multiparameter meter (Hanna Instruments, Schertz, Texas) to measure water temperature, dissolved oxygen, and specific conductance. Within the sampled area, we marked six transects perpendicular to the stream flow and equally spaced along the sampled stream reach. We measured depth and width at three points that were equally distributed along each transect and then calculated mean width and depth across the transects. We

measured the maximum current velocity of the sampled reach according to Taylor et al. (2008).

Statistical Analysis—We used fish relative abundance data normalized with the arcsine square root transformation for the following analyses. To visually assess the long-term changes (1967–2011) in seasonal fish assemblages, historical and contemporary fish assemblage data were ordinated with nonmetric multidimensional scaling (NMS). An NMS evaluates the similarities in species and environmental space by using a rank distance measure, and it is not severely affected by zero-truncation problems and nonlinearity (McCune and Grace, 2002). We removed fish species that occurred in fewer than 5% of the sample units to reduce the outlier effect (McCune and Grace, 2002). We used nonparametric multiresponse permutation procedures (MRPP) to determine whether the observed fish assemblage dissimilarities for the two groups were statistically significant (McCune and Grace, 2002). We assessed variability in seasonal fish assemblages by calculating pairwise Bray–Curtis distances for each period and then tested for mean differences with a t-test. Finally, we used indicator species analysis (ISA; Dufrene and Legendre, 1997) to identify the fish species that were indicative of each period. An ISA combines information on the relative abundance and occurrence of a species in a particular group and produces indicator values for each species in each group (Dufrene and Legendre, 1997). We used PC-ORD version 6 (McCune and Mefford, 1999) to perform NMS, MRPP, and ISA and used SYSTAT version 11 (Systat Software, Inc., Richmond, California) for the t-test.

We examined the relationships between contemporary fish assemblages and measured environmental variables by using canonical correspondence analysis (CCA; ter Braak, 1986). A CCA is a form of direct gradient analysis that links species composition to environmental factors across sample sites and provides a summary of species-environmental relationships (Rahel and Jackson, 2007). Species accounting for <0.1% of the sample set were considered rare and removed from these analyses (Miranda, 2005). We used fish abundance data for CCA after normalizing the data with a square root transformation. To meet model requirements (skewness and kurtosis <1), environmental variables excluding dissolved oxygen, mean width, and maximum velocity were log-transformed. To select environmental variables for CCA, we used a forward selection procedure (cutoff value: $P = 0.10$) with Monte-Carlo permutation tests (5,000 random permutations). Relationships between species and environmental variables were examined using a biplot based on species and environmental scores. In the ordination plot, fish species and environmental variables were represented by points and arrows, respectively, with the arrow length indicating the strength of the correlation between species scores and environmental variables. To perform CCA, we used CANOCO version 4.5 (Microcomputer Power, Ithaca, New York).

RESULTS—The fish assemblages from the two periods were structured significantly different (MRPP: $T = -9.01$, $P < 0.001$). Numerically, the assemblage of contemporary fish collections was dominated by *Cyprinella lutrensis* (58.4%), *Notropis braytoni* (16.5%), *F. zebrinus* (8.2%), *Gambusia affinis* (6.7%), and *Astyanax mexicanus* (6.0%). In contrast, the assemblage of historical fish collections was dominated by *F. zebrinus* (60.7%), *A. mexicanus*
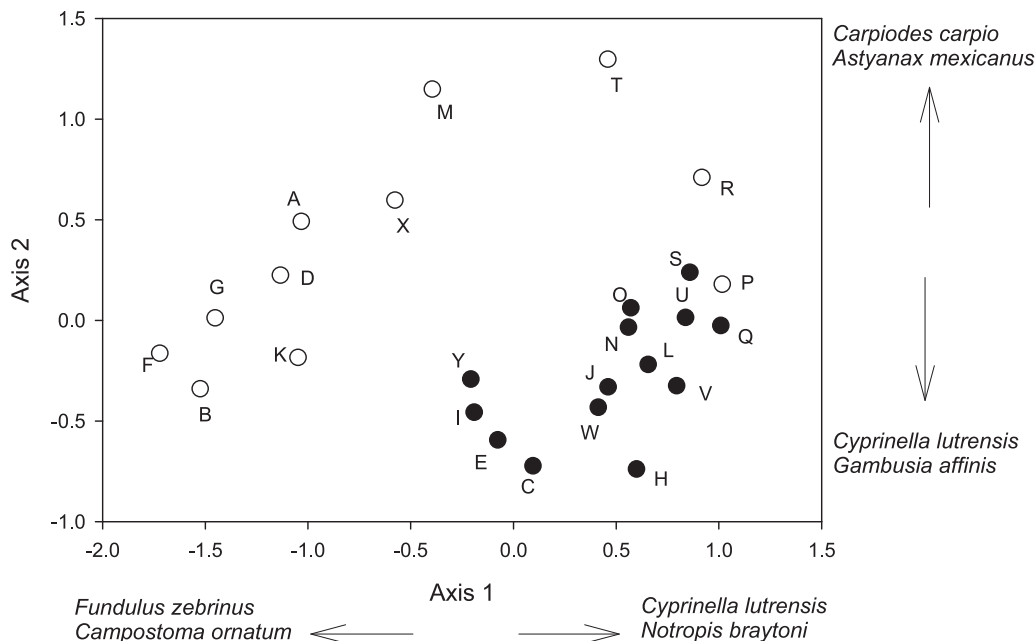
Fig. 1—Nonmetric multidimensional scaling ordination plot with contemporary (2009–2011; solid circles) and historical (1967–1970; open circles) fish relative abundance data in Tornillo Creek, Texas, United States. The capital letters in the plot indicate the capital letters of the Appendix.

(11.1%), *Carpiodes carpio* (9.9%), *Carpiodes lutrensis* (6.0%), and *Carpiodes ornatum* (5.9%). An NMS produced a two-dimensional solution for the samples (axis 1: 73.6%; axis 2: 22.6%; stress: 7.8) that separated the two time periods in multivariate space (Fig. 1). Axis 1 was positively correlated with *C. lutrensis* ($r = 0.81$) and *N. braytoni* ($r = 0.76$) and negatively correlated with *C. ornatum* ($r = -0.52$) and *F. zebrinus* ($r = -0.96$). Axis 2 was positively correlated with *Carpiodes carpio* ($r = 0.70$) and *A. mexicanus* ($r = 0.78$) and negatively correlated with *C. lutrensis* ($r = -0.52$) and *G. affinis* ($r = -0.54$) (Table 1). Contemporary fish assemblage samples clustered at the lower right portion of the plot, indicating that the contemporary samples included a higher percentage of *C. lutrensis*, *G. affinis*, and *N. braytoni* than did the historical samples. In contrast to the contemporary samples, the historical fish assemblage samples were more widely scattered in the plot, suggesting that the historical samples had much higher seasonal assemblage variability than did the contemporary samples. In historical samples, *C. ornatum* and *F. zebrinus* were abundant in winter to spring months while *N. braytoni*, *Carpiodes carpio*, *A. mexicanus*, and *C. lutrensis* were abundant in summer to fall months. A *t*-test also indicated that seasonal variability in historical fish assemblages (mean Bray–Curtis distance: 0.57) was significantly higher than that in contemporary fish assemblages (mean Bray–Curtis distance: 0.29) ($T = 8.4$, $P < 0.001$). An ISA identified *C. ornatum* as a significant indicator of the historical fish assemblages whereas four species were indicative of the contemporary fish assemblages (Table 2).

The contemporary fish assemblages were linked to several local environmental factors in Tornillo Creek. The CCA forward selection procedure retained water temperature ($F = 5.5$, $P = 0.007$), mean depth ($F = 6.2$, $P = 0.001$), and maximum velocity ($F = 2.1$, $P = 0.068$) and explained 64% of the total variation (axis 1: 51.6%; axis 2: 9.3%; axis 3: 3.1%). Axis 1 was related to water temperature ($r = -0.67$) while axis 2 was related to mean depth ($r = -0.61$) and maximum velocity ($r = -0.85$). The resulting CCA indicated that *N. braytoni* and *A. mexicanus* were abundant in warm-water months while *F. zebrinus* was abundant in cold-water months (Fig. 2). *Carpiodes carpio* and *Cyprinus carpio* were abundant in warm-water months when stream depth and velocity were

TABLE 1—Correlations of fish relative abundances with the two axes from an nonmetric multidimensional scaling with historical (1967–1970) and contemporary (2009–2011) fish assemblage data in Tornillo Creek, Texas, United States.

Species	Axis 1	Axis 2
Campostoma ornatum	−0.529	0.128
Cyprinella lutrensis	0.813	−0.528
Cyprinus carpio	0.378	−0.038
Macrhybopsis aestivalis	0.313	−0.090
Notropis braytoni	0.768	0.013
Notropis chihuahua	0.288	0.265
Pimephales promelas	0.234	0.249
Carpiodes carpio	0.448	0.709
Astyanax mexicanus	0.044	0.786
Gambusia affinis	0.290	−0.542
Fundulus zebrinus	−0.969	−0.164

TABLE 2—Result of indicator species analysis with historical and present fish assemblage data in Tornillo Creek, Texas, United States. Time periods 1 and 2 refer to historical (1967–1970) and contemporary (2009–2011) periods (respectively) and indicate the period of greatest abundance and distribution. Only significant variables are shown (based on P-values <0.05).

Species	Time	Indicator value	P
Campostoma ornatum	1	45.5	0.008
Cyprinella lutrensis	2	80.5	<0.001
Cyprinus carpio	2	42.9	0.027
Notropis braytoni	2	56.4	0.015
Gambusia affinis	2	83.1	<0.001

relatively higher. The abundances of *C. lutrensis* and *G. affinis* were negatively related to mean stream depth, indicating that these fish species were most abundant in low-flow months.

DISCUSSION—The species composition, abundances, and seasonal variation of fishes have significantly changed in Tornillo Creek between the two time periods examined in this study. This was largely due to the declining persistence and relative abundance of *C. ornatum*, a state-listed threatened species, and the increasing persistence and relative abundance of four other fish species (*C. lutrensis, G. affinis, Cyprinus carpio*, and *N. braytoni*) in the creek. Of particular importance, *C. lutrensis* has considerably increased its relative abundance. This is an example of a native, but invasive, species having a strong impact on the structure of a fish community. *Cyprinella lutrensis* is a widespread species in the southwestern United States (Matthews, 1985), and the invasion by *C. lutrensis* can have significant impacts on native fish species in a variety of ways (Douglas et al., 1994). Although *C. lutrensis* is likely a native species in the Rio Grande system (Calamusso et al., 2005), the effects of the increased dominance of *C. lutrensis* on other fish species are unknown in Tornillo Creek and require further investigation.

Notropis braytoni was the second most-abundant species (16.5% of total catch) in our collections while *N. braytoni* accounted for 4.4% of total catch of the historical samples. Hubbs et al. (2008) indicated that the distribution of *N. braytoni* was limited to the Rio Grande and Rio Conchos basins and that the abundance of *N. braytoni* had substantially decreased in the basins; thus they listed this species as one of "special concern." This species, however, has apparently increased in the mainstem Rio Grande in the Big Bend region of Texas (Carla Hassan-Williams and Timothy H. Bonner, http://www.bio.txstate.edu/~tbonner/txfishes/index.htm). In the period 1977–1993, *N. braytoni* accounted for 2.2% of the total catches in the fish collections in the mainstem Rio Grande of the Big Bend region (Hubbs et al., 1977; Bestgen and Platania, 1988; Edwards et al., 2002). In contrast, Heard et al. (2012) showed that this species accounted for 35% of their fish samples in the Big Bend reach of the mainstem Rio
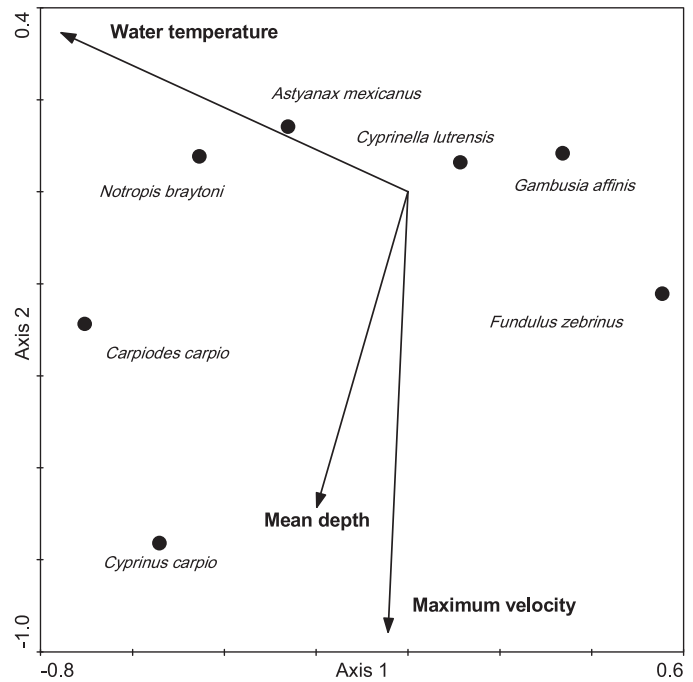

FIG. 2—Canonical correspondence analysis ordination plot with contemporary (2009–2011) fish assemblages and environmental variables in Tornillo Creek, Texas, United States. Species are represented by points and environmental variables by arrows.

Grande in 2006. *Notropis braytoni* is now also a dominant species in lower Terlingua Creek in the region (Miyazono and Taylor, 2013b). Our results suggest that the abundance of *N. braytoni* might have increased not only in the mainstem Rio Grande but also in its tributaries in the Big Bend region.

We predicted that the relative abundance and persistence of *F. zebrinus* would have increased in Tornillo Creek. However, the results of ISA indicated that *F. zebrinus* was not indicative of the contemporary fish assemblages. This was because the relative abundance of *F. zebrinus* declined in the creek relative to the overwhelming increase in the relative abundance of *C. lutrensis* and *N. braytoni*. In contrast, the persistence of *F. zebrinus* has increased in Tornillo Creek (Miyazono and Taylor, 2013a). *Fundulus zebrinus* occurred in nine of the 11 fish collections in the historical samplings but occurred in all our collections. Hubbs and Wauer (1973) hypothesized that *F. zebrinus* and *C. ornatum* may experience intense food competition because both species have long intestines and similar seasonal habitat use in the creek. Although these species utilize different microhabitats, exploitative competition could be an important mechanism leading to the resulting patterns. The first capture of *F. zebrinus* in the region was in 1954, and *C. ornatum* was the most-abundant species at that time (Hubbs and Wauer, 1973). In the period 1967–1970, *F. zebrinus* was the most-dominant fish in the creek while the relative abundance of *C. ornatum* was 5.9% of the total

catch (Hubbs and Wauer, 1973). In the period of 2009–2011, *C. ornatum* did not occur in our collections while *F. zebrinus* was still abundant in the creek. These results suggest that *F. zebrinus* has largely replaced *C. ornatum* in Tornillo Creek.

Campostoma ornatum is an herbivore (Contreras-Balderas, 1974) whereas *F. zebrinus* is likely planktivorous (Linam and Kleinsasser, 1988; Miller and Robison, 2004). In addition, responses to environmental conditions likely differ between the two species (Linam and Kleinsasser 1988). *Fundulus zebrinus* tend to be more tolerant to low dissolved oxygen concentrations than are *C. ornatum* (Linam and Kleinsasser 1988). Changes in water quality conditions might have affected the persistence of these two species in Tornillo Creek. Thus, further research on environmental factors affecting these two species is needed in the region.

Contemporary seasonal fish assemblage patterns were linked to several environmental factors in Tornillo Creek. The results of CCA indicated that water temperature was a strong predictor of contemporary fish assemblage patterns and a driver of seasonal change in the creek. Hubbs and Wauer (1973) also found strong seasonality of fish assemblages in the period 1967–1970. For example, the shiners (*C. lutrensis*, *N. braytoni*, and *Notropis chihuahua*) and *Carpiodes carpio* were abundant in warm months while *C. ornatum* and *F. zebrinus* were abundant in the creek in cold months (Hubbs and Wauer, 1973). In our study certain fish taxa, such as *N. braytoni*, *F. zebrinus*, and *Carpiodes carpio*, followed the historical seasonal abundance patterns shown by Hubbs and Wauer (1973) whereas *C. lutrensis* did not conform to their general pattern because of its high contemporary persistence and abundance in the creek. The fish assemblages of both time periods were highly variable, but there has been a definite shift, suggesting a new equilibrium regarding seasonal fish assemblage composition and variability in Tornillo Creek.

The contemporary abundances of *Carpiodes carpio* and *Cyprinus carpio* were positively related to mean stream depth and current velocity. Because all *Carpiodes carpio* and *Cyprinus carpio* caught in Tornillo Creek were juvenile, these species could ascend tributaries from the Rio Grande in high-flow months in search of nursery habitats (Hubbs and Wauer, 1973). In contrast, *C. lutrensis* and *G. affinis* were most abundant in low-flow months, suggesting that these two species might be tolerant of decreased stream flow. We could not examine relationships between the seasonal fish assemblage dynamics and flow regime in Tornillo Creek because there were not stream flow data for the creek. However, we suggest that the maintenance of stream flow and connectivity to the mainstem are important for the immigration and emigration of certain riverine fishes in Tornillo Creek and that decreases in stream flow will accelerate the domination of the tolerant species.

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APPENDIX—Fish relative abundances (%) of historical (1967–1970) and contemporary (2009–2011) data in Tornillo Creek, Texas, United States. The capital letters in this table correspond with the capital letters in Figure 1.

| | Sample date | | | | | | | | | | | | |
Sample ID	A 29 January 1969	B 6 January 1970	C 22 January 2011	D 26 February 1969	E 19 February 2011	F 28 March 1969	G 18 March 1970	H 17 March 2010	I 13 March 2011	J 30 April 2011	K 6 May 1969	L 25 May 2011	M 10 June 1969	N 8 June 2011
Campostoma ornatum	0	17.2	0	0	0	0	5.0	0	0	0	4.8	0	7.2	0
Cyprinella lutrensis	0	0.5	72.5	0	45.8	0	0	88.6	44.2	61.1	2.4	61.3	0	53.6
Cyprinus carpio	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1
Hybognathus amarus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Macrhybopsis aestivalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Notropis braytoni	0	0	0	0	0	0	0	2.5	0	7.3	0	21.9	0	22.3
Notropis chihuahua	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pimephales promelas	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhinichthys cataractae	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0
Carpiodes carpio	0	0	0	0	0	0	0	0	0	1.9	8	2.6	40.2	2.5
Cycleptus elongatus	0	0	0	0	0	0	0	0	0	0	2.4	0	0	0
Moxostoma congestum	0	0	0	0	0	0	0	0	0	0	0	0	8.2	0
Astyanax mexicanus	34.1	0	0	16.9	0.4	0	2.7	0.2	0.6	2.5	0	3.6	26.8	12.4
Ictalurus punctatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gambusia affinis	1.2	0	4.5	1.7	23.2	0	0	4.3	12.5	16.2	2.4	5.8	1.0	3.1
Fundulus zebrinus	64.6	82.4	22.9	81.4	30.5	100	92.3	4.2	42.7	11.1	80	4.8	16.5	6.0
Oreochromis aurea	0	0	0	0	0	0	0	0	0	0	0	0	0	0

APPENDIX—Continued.

	Sample date										
Sample ID	O 21 July 2011	P 9 August 1967	Q 18 August 2010	R 18 September 1969	S 18 September 2010	T 20 October 1967	U 16 October 2010	V 19 November 2009	W 20 November 2010	X 29 December 1967	Y 18 December 2010
Campostoma ornatum	0	0	0	0.4	0	0	0	0	0	0	0
Cyprinella lutrensis	43.9	61.4	64.6	21.8	42.8	13.7	40.2	64.5	73.5	9.4	47.5
Cyprinus carpio	0.1	0	0.09	0	0.3	0	2.1	0	0.4	0	0
Hybognathus amarus	0	0	0.09	0	0	0	0	0	0	0	0
Macrhybopsis aestivalis	0	0	0.09	0	0	0	0	0.05	0	0	0
Notropis braytoni	18.8	9.1	17.8	29.7	32.6	0	34.0	21.3	3.8	0	0
Notropis chihuahua	0	0	0.09	0.8	0	0	0	0	0	0	0
Pimephales promelas	0	0	0	3.8	0	0	0	0	0.1	0	0
Rhinichthys cataractae	0	0	0	0	0	0	0	0	0	0	0
Carpiodes carpio	2.2	13.6	11.8	40.2	19.5	33.3	12.4	0.9	0.1	0	0
Cycleptus elongatus	0	0	0	0	0	0	0	0	0	0	0
Moxostoma congestum	0	0	0	0	0	0	0	0	0	0	0
Astyanax mexicanus	20.9	15.9	4.6	2.1	2.5	52.9	2.2	2.1	4.9	52.8	3.0
Ictalurus punctatus	0	0	0.4	0	0	0	0	0	0	0	0
Gambusia affinis	10.9	0	0.09	0.4	0.10	0	7.0	9.5	6.6	0	2.6
Fundulus zebrinus	3.2	0	0.3	0.8	2.3	0	1.9	1.7	10.6	37.8	46.9
Oreochromis aurea	0	0	0	0	0	0	0.1	0	0	0	0