

Response of Endangered Desert Fish Populations to a Constructed Refuge

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Abstract

The U.S. Bureau of Reclamation created a shallow, 110-m channel to provide habitat for two endangered fishes, *Cyprinodon elegans* (Comanche Springs pupfish; Cyprinodontidae) and *Gambusia nobilis* (Pecos gambusia), at the site of the fishes' former natural habitat. The ciénega (marsh) associated with Phantom Lake Spring in Jeff Davis County, Texas, was destroyed by the creation of an irrigation canal system. In 1993, the endangered fishes were stocked into the refuge with individuals from the irrigation canals, and in the case of *C. elegans*, hatchery stocks. The condition of habitat, status of fish populations, and fish ecology within the refuge were then monitored for two years. The abundance and density of both species increased in accordance with aquatic plant development. *Cyprinodon elegans* abundance peaked after one year and stabilized at an average density of 14.7/m² by the end of our study. Juvenile *C. elegans* were always rare, which may indicate that the population reached the refuge's carrying capacity and that recruitment is low. *Gambusia nobilis* was the most abundant fish in the refuge (average density 96/m²), used the entire refuge, and outcompeted nonindigenous *G. geiseri*. The two *Gambusia* species used similar habitats but showed almost no dietary overlap. High densities of aquatic plants reduced the amount of open water areas necessary for *C. elegans*. The refuge will sustain the two endangered fishes at this historic site of endemism while maintaining flow to the irrigation system; however, the refuge is not equivalent to a restored ciénega.

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Introduction

Cyprinodon elegans (Comanche Springs pupfish; Cyprinodontidae) and *Gambusia nobilis* (Pecos gambusia; Poeciliidae) are federally listed endangered species that inhabit spring-fed surface waters of the Pecos River basin in western Texas. *Cyprinodon elegans* was discovered in 1853 in the ciénega (spring-fed sloughs and marshes) of Comanche Springs, Pecos County, Texas, but it was extirpated from this region in 1955 when the springs dried up in response to excessive withdrawal of water from the Edwards-Trinity aquifer (Fig. 1). Currently, *C. elegans* persists in the Reeves County Water Improvement District's irrigation canals and the associated springs in the vicinity of the towns of Toyahvale and Balmorhea in Reeves and Jeff Davis Counties (Hubbs et al. 1991). *Gambusia nobilis* also inhabits the Toyahvale-Balmorhea canals and springs and also occurs in Leon Creek and the Diamond-Y Springs in Pecos County, Texas. *Gambusia nobilis* was extirpated from Comanche Springs (Hubbs et al. 1991) and is limited to tributaries of the Pecos River in Texas and New Mexico (Lee et al. 1980).

In Reeves and Jeff Davis Counties, the historical habitat of both fishes was a network of ciénegas supported by Phantom Lake Spring, San Solomon Spring, Giffen Spring, and East and West Sandia Springs. In the arid southwest of North America, ciénegas are critical ecosystems for aquatic organisms and for a great number of terrestrial plants and animals (Hendrickson & Minckley 1984). Phantom Lake Spring emerges from a small cave at the base of a limestone bluff located approximately 6 km west of Toyahvale in Jeff Davis County near its border with Reeves County. The spring discharge is immediately channeled into the Reeves County Water Improvement District's irrigation canals. Due to its relatively



Figure 1. Endangered species *Cyprinodon elegans* (Comanche Springs pupfish; Cyprinodontidae). Total length is approximately 6 cm.

high elevation (1080 m), Phantom Lake Spring is vulnerable to reductions in the aquifer from water withdrawal. The spring discharge has declined steadily over the past 60 years (Young et al. 1993). The spring was an important resource for indigenous peoples; however, diversion of the spring outflow for irrigation was initiated in the 1870s for production of crops for military units at nearby Fort Davis (Young et al. 1993). In 1914, the many local canal companies were consolidated into the Reeves County Water Improvement District No. 1. In 1946, the district's facilities were reconstructed by the U.S. Bureau of Reclamation. The Bureau of Reclamation received ownership of 7.1 ha surrounding Phantom Lake Spring as part of the agreement for reconstruction of the district's facilities. Previously, Phantom Lake Spring discharged into a small lake (ca. 10 ha) that drained into another underground system that is now dry.

Creation and Stocking of the Refuge

The concrete irrigation canal that drains the springhead has vertical walls and a small amount of shallow water habitat used by the smaller fishes endemic to the region. Following the enactment of the Endangered Species Act (ESA) and the subsequent designation of *C. elegans* and *G. nobilis* as endangered species, the Bureau of Reclamation consulted the U.S. Fish and Wildlife Service and the Rio Grande Fishes Recovery Team to design, construct, and monitor a native fish refuge channel at Phantom Lake Spring (Rio Grande Fishes Recovery Team 1981, 1983). The goal of the project was to establish a channel outside of the existing irrigation canal that would maintain flows to the irrigation system yet provide structurally diverse, shallow-water habitat for native fishes. At the outset, Bureau of Reclamation planners met with the Reeves County Water District to achieve compatibility between the project and irrigation needs and water rights. Bureau of Reclamation engineers designed the refuge in consultation with other staff and in compliance with the National Environmental Policy and Endangered Species Acts (Young et al. 1993). The project was funded through Public Law (102-27, Emergency Drought Assistance Act (Young et al. 1993).

Construction of the refuge began in February 1993, and water was first diverted from the springhead/irrigation canal into the structure in June 1993. The refuge is a 110-m channel excavated parallel to the concrete irrigation canal (Fig. 2). To minimize water loss, the channel was lined with a sheet of low density polyethylene. Two large (6 × 6 m) and two small pools (4 × 4 m) were formed along the longitudinal axis of the channel, each separated by runs of approximately 10 × 3 m. The channel bottom was terraced along the entire length of the channel (15 cm vertical rise with the deepest region



Figure 2. The Phantom Lake Spring irrigation canal and endangered fish refuge in November 1993. This view is from just above the spring outflow looking toward the Cipoletti weir that controls the exit of water from the refuge.

adjacent to the wall of the irrigation canal). Soil excavated from the refuge channel was placed in the refuge to provide a natural substrate. At flows less than or equal to $0.3 \text{ m}^3/\text{s}$, evaporative losses were estimated to be lower in the refuge than the irrigation canal; the refuge flow capacity is approximately $0.4 \text{ m}^3/\text{s}$ (Young et al. 1993). Spring discharge greater than $0.4 \text{ m}^3/\text{s}$ spills into the irrigation canal and onto the ground near the refuge. Leakage from the droplog structure separating the refuge channel from the original *ciénega* site plus seepage from the adjacent limestone bluffs has created a shallow pool (*ciénega*) that fluctuates in depth (ca. 15–30 cm) and area (ca. 100–400 m^2). Refuge water depth and water exit from the refuge outlet can be controlled with an adjustable aluminum Cipoletti weir. This weir is elevated above the irrigation canal so that a small waterfall restricts the movement of most fishes into the refuge. The exception was native *Astyanax mexicanus* (Mexican tetra; Characidae), which is an active swimmer that is capable of leaping over the waterfall. The weir was adjusted to maintain a flow a little greater than $0.1 \text{ m}^3/\text{s}$,

a rate that does not displace the unconsolidated substrate yet maintains maximum wet area (Young et al. 1993). A floating grid of PVC pipe was installed below the waterfall, and this appears to have restricted entrance by *A. mexicanus* from below the refuge (Young et al. 1993) but probably has not eliminated it (our conclusions, see Discussion below). In June 1993, aquatic vegetation and associated invertebrates from the local canals were transferred into the refuge, and these became established and grew over the summer.

On September 20–21, 1993, members of the Rio Grande Fishes Recovery Team seined the lower canals of the region and obtained two *C. elegans* and 135 *G. nobilis*, which were transferred to the refuge. An additional 109 *C. elegans* obtained from the Uvalde Federal Fish Hatchery were stocked in the refuge on October 14, 1993. The hatchery fishes were first screened by the Texas Parks and Wildlife Department for genetic verification of species identity. Genetic divergence among subpopulations of *C. elegans* was documented by Echelle (1975; Echelle et al. 1987). The Uvalde fish are derived from 73 individuals collected from the Phantom Lake Springs ciénega when it flooded in 1990 (G. Garrett, Texas Parks and Wildlife Department, personal communication). We were contracted by the Bureau of Reclamation to determine fish population dynamics and patterns of habitat use within the refuge for a period of two years. In addition to reporting those findings, we offer management recommendations and briefly discuss the suitability of constructed refuges, such as the one at Phantom Lake Spring, for species conservation.

Methods

The Phantom Lake Spring refuge was surveyed quarterly for two years: November 6 & 7, 1993; February 5 & 6, 1994; May 14 & 15, 1994; August 25 & 26, 1994; November 5, 1994; February 18, 1995; May 13, 1995; and August 10 & 11, 1995. With the exception of the second and last surveys when measurement of habitat attributes began at approximately 1700 hours, habitat measurements (including dissolved oxygen measurements) were initiated between 0915 and 1200 hours. Except for the second and last surveys when fish estimates began at 0830 and 1000 hours, respectively, fish estimates were made between 1300 and 1800 hours. Salinity, conductivity, and pH were measured at the inflow and outflow of the refuge during each survey. Salinity and conductivity were measured with a YSI® conductivity meter. Habitat and fishes were sampled at nine transects that ran perpendicular to the refuge channel. Transects 1, 3, 5, and 7 were located in simulated runs, transects 2 and 6 were located in large pools, transects 4 and 8 were located in small pools, and transect 9 passed

through the center of the rectangular pool adjacent to the refuge outflow. At each transect, temperature ($\pm 0.1^\circ\text{C}$) and dissolved oxygen ($\pm 0.1\text{ mg/l}$) were measured near the substrate at midchannel and edge with a YSI® conductivity meter and pH meter, respectively. Beginning from a point 0.25 m from the wall of the irrigation canal, water depth was measured each 0.5 m along each transect. Beginning from a point 0.75 m from the wall of the irrigation canal, water current velocity near the surface (1/3 depth) and above the substrate (2/3 depth) was measured each 1.0 m along each transect with a Flow-Mate® digital electronic flow meter ($\pm 0.01\text{ m/s}$). The rate of water discharge from the refuge was calculated from the elevation of water at the Cipoletti weir (Young et al. 1993).

During the first three surveys, habitat structure (percent area coverage of vegetation and substrate categories) was visually estimated for a 1-m wide rectangle centered on each transect. The substrate categories were cobbles, stones, sand, and silt. The vegetation categories were *Typha latifolia* (cattails), *Scirpus* sp. (bulrush), *Chara* sp. (chara), and *Cladophora* sp. (filamentous algae). During the final five surveys, a 1-m² PVC frame divided into a grid of 100-1-cm² squares was overlaid near midchannel at each transect, and habitat structure was estimated by counting the number of squares dominated by each vegetation and substrate category.

During each survey, the number of individuals of each fish species was counted within a 1 m wide rectangle centered on each transect. For all transects on a given sampling date, these counts were made one transect at a time by a stationary shoreline observer. Observation time for each transect was approximately 15 minutes, and transects were observed consecutively. During the final four surveys, fish densities were estimated at each transect using a 1-m³ throw trap. This technique is particularly effective for sampling fishes in shallow, vegetated areas (Kushlan 1981). The trap was covered by a 0.2-mm mesh fiberglass screen on four sides and was open on two opposing sides. The perimeter of one of the open ends of this box was weighted. The trap was thrown once over the middle of a transect, and the weighted end was quickly secured against the substrate so that no fishes could escape during removal with dip nets. We noted no escapement once the trap was secured; however, a small percentage of fishes probably managed to avoid the trap before it reached the substrate. Though minor, this avoidance was probably greater for *C. elegans* and *A. mexicanus* and very negligible for the two *Gambusia* species. We have no reason to expect that trap avoidance varied systematically between locations and seasons. Once secured, all fishes were removed from the trap with dip nets and placed into buckets containing water from the refuge. All fishes were identified to species and, except for *A. mexi-*

canus, categorized as either adult male, adult female, or immature. Sexual dimorphism is obvious in both species (male gonopodia (modified anal fin) in *Gambusia* spp., male coloration in *C. elegans*). Potential relationships between species abundance (total collected per sample date) and environmental variables were examined using the general linear models regression procedures of SAS (SAS Institute 1989). Critical p values were adjusted by the Bonferroni method: $p = 0.05/n$, where n is the number of related statistical comparisons.

To permit evaluation of its potential role as a competitor or predator of the two endangered fishes, we sacrificed all *A. mexicanus* captured during our visits to the refuge. The U.S. Fish and Wildlife Service granted us permission (subpermit under PRT-676811) to sacrifice up to 20 individuals of *C. elegans* and *G. nobilis* for closer laboratory examinations. Standard length (SL), sex, and stomach contents were recorded for subsamples of *C. elegans*, *G. nobilis*, and *G. geiseri* captured during the final survey and for all *A. mexicanus* taken throughout the study. The volume of each diet item from stomach contents was estimated by water displacement in graduated cylinders. Diet items were then summed across specimens for each species and converted to volumetric percentages of the total food consumed by the species.

Results

Habitat Dynamics

Dissolved oxygen declined in the refuge during the two winter samples and showed an overall increase of approximately 2 mg/l within the refuge during the second year of the survey (Fig. 3). Temperature was relatively constant at about 25°C, especially at midchannel (Fig. 3).

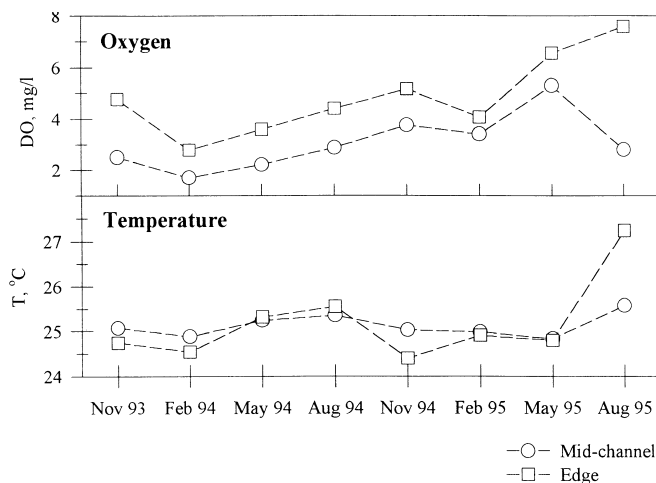


Figure 3. Temporal variation in mean dissolved oxygen and water temperature near midchannel and edge of the Phantom Lake Spring refuge.

The highest temperatures were recorded from shallow edge areas during the August 1995 survey, the only survey when measurements were made during the afternoon. Except for the August 1995 sample that shows an increase in temperature at the downstream refuge transects, temperature tended to remain relatively constant over the longitudinal gradient of the refuge (Fig. 4). In contrast, dissolved oxygen increased over the longitudinal gradient during all survey periods (Fig. 4). Salinity was nearly constant at 1.9–2.0 ppt across all transects and survey dates, and conductivity ranged from 2900–3700 μ mhos. On a given survey date, pH did not vary more than 0.1 between transect 1 and 9. With the exception of the afternoon measurements taken on the final survey, pH averaged between 6.5 and 7.5. The final August survey pH was 8.5, and this higher value probably resulted from the influence of rapid photosynthesis by aquatic plants on dissolved carbon dioxide.

To our knowledge, no adjustments were made to the Cipoletti weir, and any variation in water discharge from the refuge would have been a function primarily of outflow from the spring and secondarily of vegetation impediment of flow and overflow into the remnant ciénega basin. During the initial surveys when plant growth was sparse, water velocities tended to be greatest in the deep channel region nearest the wall of the irrigation canal and velocities were slowest in shallow areas near the opposing bank. As plant biomass increased, flow near the substrate was greatly curtailed, and flow near the surface was less predictable as water was diverted around regions of dense vegetation. The dense cattail growth surrounding transects 2 and 3 had the greatest influence on water velocity. For example, a greater temporal decline in the maximum water velocity was observed at transect 3 compared to transect 5,

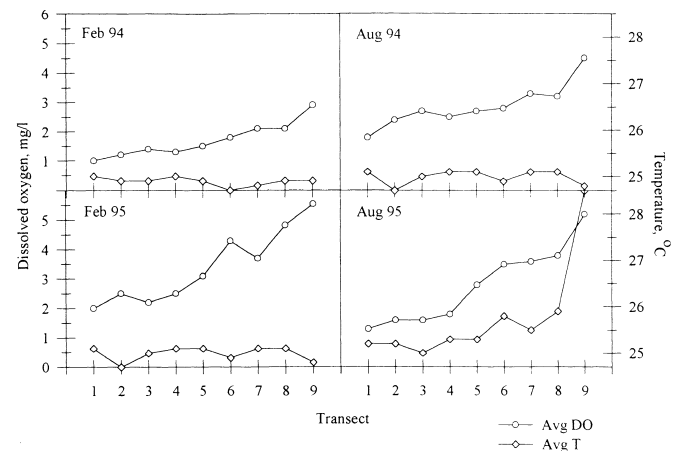


Figure 4. Dissolved oxygen and temperature at nine transect locations (1 = nearest the spring outflow, 9 = nearest the Cipoletti weir) during four survey dates.

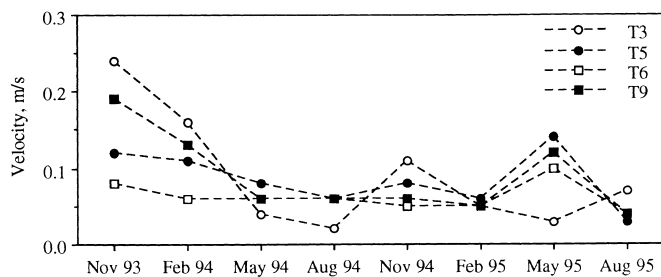


Figure 5. Maximum water velocities recorded at four transects: T3 = run just downstream from the pool (T2) that became dominated by *Typha*, T5 = run in the downstream reach of the refuge, T6 = large pool just downstream from T5, and T9 = transect running perpendicular to the refuge outflow.

located at a similar run farther downstream (Fig. 5). During the early stages of aquatic plant development, pool regions tended to have slower velocities than runs (e.g., T6 versus T3 and T5; Fig. 5).

The substrate did not appear to shift in response to water flow, and the primary change in substrate was the gradual accumulation of silty organic matter in regions of slow flow. Aquatic vegetation increased from a mean of approximately 70% coverage in both pool and run transects during the initial survey to greater than 90% coverage during the August 1994 survey and all subsequent surveys (Fig. 6). During the first year, bulrush and the alga *Chara* dominated the refuge. During the second year of our survey, plant species richness (*S*) ranged from 1 to 3 for most transects. Bulrush and filamentous algae dominated most of the refuge; however, *Chara* remained the dominant plant at transect 9, and a dense stand of cattails completely overtook the large pool at transect 2 (Table 1). By the time of our final survey (August 1995), cattails had attained 100% coverage at transect 3. Except for transects 2 and 3 (the only places where cattails occurred), plant diversity tended to be relatively high throughout the refuge during the summer and fall (H' range = 0.39–0.85; based on data collected using the grid method). During winter and spring, plant diversity decreased at some transects (H' range = 0–0.78, excluding transects 2 and 3). For example, H' was 0 at transects 7 (bulrush), 8 (bulrush), and 9 (chara) during February 1995.

Population Status and Ecological Relationships

Initially, all species were rare in the refuge; densities based on visual estimates by a shoreline observer were greater than 20 individuals per species. By the time of the last survey, the two endangered species, *Cyprinodon elegans* and *Gambusia nobilis*, were the most abundant fishes in the refuge (Fig. 7). The apparent decline in *C. elegans* during the second year could have been influ-

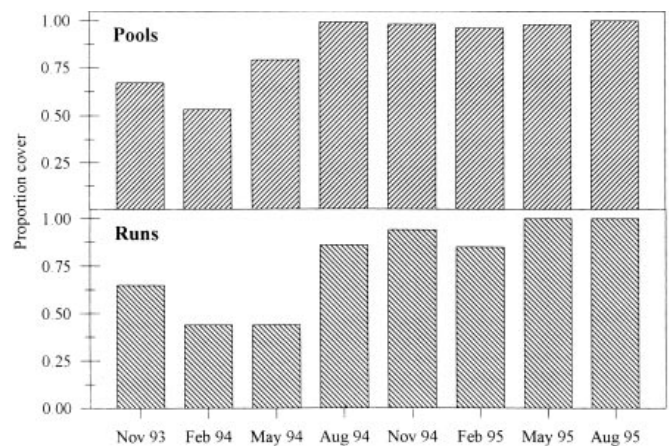


Figure 6. The proportion of vegetation cover in surveyed pool and run locations of the Phantom Lake Spring refuge throughout the survey period.

enced by the different sampling methods employed during the first and second years. However, our shoreline observations during the second year resulted in *C. elegans* counts per transect that were comparable to those derived from the throw trap method (e.g., 116 counted visually in August 1995, compared with 132 captured in the throw trap the same day). We concluded that the two methods were equivalent in censusing populations per transect even though they sampled different areas. During the second year, the *C. elegans* population was strongly dominated by adult females (Table 2). Given that males are highly territorial and the species can breed virtually year-round, this skewed sex/age structure may indicate that the population was near its carrying capacity within the refuge. Because fishes were not captured and handled during the first year of the survey, their population age structures could not be documented. The abundance of *G. nobilis* increased markedly following the first winter in the refuge, and it remained the most abundant fish species throughout the survey period (Fig. 7). The *G. nobilis*

Table 1. Percent vegetational composition at each transect during the second year of sampling (4 surveys) in the Phantom Lake Spring refuge.

Transect	<i>Cladophora</i>	<i>Chara</i>	<i>Scirpus</i>	<i>Typha</i>
1	38.8	1.2	59.9	0
2	0	0	0	100
3	33.6	1.2	39.4	25.8
4	63.0	3.0	34.0	0
5	60.8	0.3	39.0	0
6	57.0	17.5	25.5	0
7	54.0	0	46.0	0
8	35.2	1.5	63.3	0
9	21.5	78.1	0.4	0

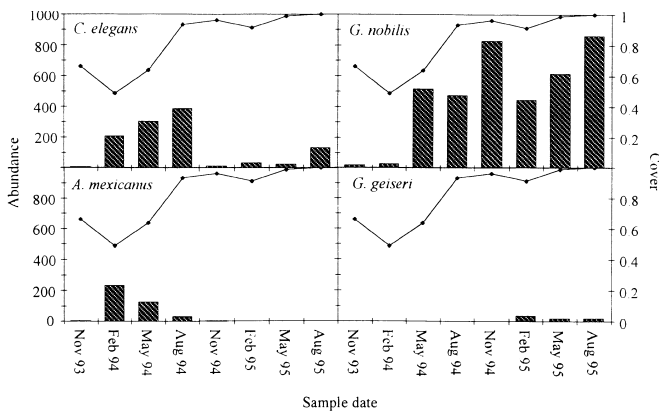


Figure 7. The total abundances per sample date (bars) of the four fish species in the Phantom Lake Spring refuge during the survey period. Bars before November 1994 are sums based on visual counts of free ranging fishes by a shoreline observer at 9 transects, and bars on or after November 1994 are sums of counts from throw trap samples at nine transects. Line plots are percentage coverage of aquatic vegetation based on nine transects.

population was dominated by adult females, and juveniles were common during most periods (Table 2). The abundance of *A. mexicanus* within the refuge peaked in February 1994, and this species was extremely rare during the second year (neither visual counts nor trap samples revealed >23 individuals/survey). An active swimmer with leaping ability, *A. mexicanus* can pass freely between the refuge and the spring outflow and probably between the refuge and the irrigation canal system as well. *Gambusia geiseri* was not intentionally stocked in the refuge and was very rare throughout the two year survey. A single male *G. geiseri* was taken in the November 1994 throw trap samples, and the abundance of *G. geiseri* peaked at 36 in February 1995 (Fig. 7). Female *G. geiseri* outnumbered males, and juveniles were rare and taken in only one of four trap surveys (Table 2).

Based on fish counts from trap samples, the three small species were distributed throughout the refuge, whereas *A. mexicanus* was restricted to the deepest regions containing pockets of open water (Table 3). Rela-

Table 2. The abundance (total collected per date), sex ratio, and percentage of juveniles of three fish species from throw trap samples at the Phantom Lake Spring refuge.*

Date	<i>C. elegans</i>			<i>G. nobilis</i>			<i>G. geiseri</i>		
	N	F (%)	J (%)	N	F (%)	J (%)	N	F (%)	J (%)
Nov 94	11	90.0	9.1	831	62.3	32.3	2	50.0	0
Feb 95	34	85.3	0	446	80.4	20.0	37	66.7	2.7
May 95	25	88.0	0	415	72.8	7.7	19	78.9	0
Aug 95	132	57.4	12.9	863	68.3	27.2	22	77.3	0

*N indicates total collected per date; F, sex ratio; J, percentage of juveniles.

Table 3. Fish species distributions (percent composition) across transects during the second year of sampling (throw traps) in the Phantom Lake Spring refuge.

Transect	<i>C. elegans</i> (%)	<i>G. nobilis</i> (%)	<i>G. geiseri</i> (%)	<i>A. mexicanus</i> (%)
1	10.4	13.9	1.3	0
2	0.5	2.3	1.3	0
3	2.5	11.4	1.3	11.1
4	56.4	16.5	28.8	66.7
5	7.9	12.5	13.8	0
6	8.4	13.1	18.8	0
7	4.0	13.6	13.8	0
8	5.4	7.1	8.8	0
9	4.5	9.7	12.5	22.2

tive abundances for all four fish species were particularly high in the small pool at transect 4 (Table 3), an area dominated by *Scirpus* and filamentous algae. All possible combinations of species abundance and environmental variables were regressed (based on all nine transects and all eight sample dates), and only *G. nobilis* yielded statistically significant regressions. *G. nobilis* abundance was positively associated with aquatic vegetation cover ($r = 0.449$, $df = 71$, $p < 0.0001$) and negatively associated with water velocity near the surface ($r = -0.517$, $df = 71$, $p < 0.0001$) and the rate of water discharge from the refuge ($r = -0.443$, $df = 71$, $p < 0.0001$). *Gambusia nobilis* was also positively associated with *G. geiseri* ($r = 0.357$, $df = 72$, $p < 0.01$).

Cyprinodon elegans consumed mostly filamentous algae and a lesser number of *Cochliopa texana* (snails) (Table 4). *Gammarus hyalelloides* (amphipods) comprised nearly three-fourths of the diet of *G. nobilis*, followed by much smaller amounts of filamentous algae, ostracods, and microscopic items (Table 4). In contrast, *G. geiseri* consumed mostly diatoms, filamentous algae, and detritus (Table 4). *Astyanax mexicanus* consumed a variety of plant and animal prey, especially filamentous algae and insects (Table 4).

Discussion

The Phantom Lake Spring refuge was designed as a compromise solution that provides a partially restored ciénega habitat at its original location, yet allows maintenance of customary water flow to irrigation canals with minimal evaporative loss. Based on information gathered for two years subsequent to the initial stockings of endangered fishes in the refuge, the U.S. Bureau of Reclamation's constructed habitat appears to provide a very favorable environment for *Cyprinodon elegans* and *Gambusia nobilis*. The two species have increased their density and abundance, and at least some individuals of each species can now be encountered through-

Table 4. Diets of fish species inhabiting the Phantom Lake Spring refuge.

	<i>Cyprinodon elegans</i> n = 20		<i>Gambusia nobilis</i> n = 17		<i>Gambusia geiseri</i> n = 21		<i>Astyanax mexicanus</i> n = 24	
	Frequency	% Volume	Frequency	% Volume	Frequency	% Volume	Frequency	% Volume
diatoms	0	0	1	0.2	15	43.2	0	0
filamentous algae	20	86.0	3	8.5	14	20.5	9	51.6
macrophytes	0	0	0	0	0	0	5	3.1
seeds	0	0	0	0	2	5.8	1	1.1
detritus	0	0	3	4.0	14	13.6	0	0
protozoa	0	0	1	5.4	6	7.5	0	0
rotifers	0	0	0	0	1	1.1	0	0
invertebrate eggs	0	0	1	1.4	4	4.1	0	0
Amphipoda ^a	0	0	12	73.7	1	0.5	2	5.0
Cladocera	0	0	0	0	1	0.8	0	0
Ostracoda	0	0	1	6.9	5	2.3	0	0
snails ^b	9	14.0	0	0	0	0	3	6.1
insects ^c	0	0	0	0	6	0.5	11	26.3
Total Volume (ml)	6.35		0.65		1.47		2.70	

^a Amphipoda are *Gammarus hyalelloides*.

^b Snails are *Cochliopa texana*.

^c Insects includes Diptera (chironomid larvae), Coleoptera, Ephemeroptera, Hymenoptera (ants), and Plecoptera.

out the refuge. *Gambusia nobilis* in particular is thriving at high densities (30–144 individuals/m²). The density of *C. elegans* seems to have peaked at 0–150 individuals/m² just after the first year of residence in the refuge and may have stabilized with an adult dominated population of 0–91 individuals/m² (average = 14.7/m²).

Increases in the total abundance of the two endangered species during the first year coincide with increases in aquatic vegetation biomass (Figure 7). Filamentous algae serve as the primary food resource for *C. elegans*, and aquatic vegetation indirectly supports the *G. nobilis* because it harbors the amphipods and other tiny invertebrates on which it feeds. In addition, aquatic vegetation undoubtedly provides a refuge from predators for juveniles of both species. Very high densities of aquatic plants, such as those now encountered within the refuge, could have a detrimental effect on *C. elegans* abundance. The stands of cattails that developed at transects 2 and 3 retard aquatic production via shading (we noted no significant algal growth at these transects during the final survey), dissolved oxygen generation, water velocity, and drifting prey. During our final survey, the density of *G. nobilis* was relatively low at transect 2 (46/m²), and no *C. elegans* were captured or observed there. *Cyprinodon elegans* seems to require a patchy habitat containing areas of dense vegetation that serves as a refuge from predators and areas of open water where filamentous algae (periphyton) can grow on submersed surfaces and where courtship and spawning can take place. Open water areas may actually be more important for *C. elegans* than vegetation.

The presence of *Astyanax mexicanus*, a native fish of this region, does not appear to pose an appreciable

threat to the long-term persistence of either endangered fish population. We presume that *A. mexicanus* can move more or less freely between the refuge and the spring outflow and irrigation canal. Although our sample was too small to document piscivory, *A. mexicanus* is known to be an opportunistic omnivore, and this was confirmed by our dietary data from fish captured within the refuge (Table 4). *A. mexicanus* essentially is an algae grazer and drift feeder, and our data suggest that its overall abundance within the refuge is regulated primarily by the amount of deeper open-water areas. As aquatic vegetation density increased in the refuge, *A. mexicanus* abundance declined.

While not desired, the presence of *Gambusia geiseri* in the refuge does not appear to pose an immediate threat to *G. nobilis*. To date, *G. nobilis* appears to outcompete *G. geiseri* within this habitat. These two congeners demonstrated almost no overlap in diet (Table 4). We observed no evidence of hybridization between the two congeners, and this is consistent with Hubbs and Springer's (1957) finding of the two populations coexisting in Comanche Springs and in the canals near Toyahvale.

Following the life history framework of Winemiller (1992; Winemiller & Rose 1992), *C. elegans* and *G. nobilis* both could be characterized as opportunistic species. Both species mature at small sizes within one year, have prolonged breeding periods (perhaps year-round in stenothermal spring outflows), and have relatively short interbrood intervals (days in *C. elegans*, weeks in *G. nobilis*). All of these factors tend to elevate the intrinsic rate of natural increase and enable these populations to rapidly recolonize recently disturbed habitats. These populations are probably best viewed from the perspective

of metapopulation dynamics. As long as remnants of suitable habitat remain somewhere on the landscape and at least some level of migration between remnant patches is achieved, then populations of these fishes should be highly resilient to short-term, local disturbances (Winemiller & Rose 1992; Van Winkle et al. 1993). Historically, the springs and ciénegas of the Balmorhea area constituted a dynamic mosaic of shallow aquatic habitats. During times of drought, aquatic populations probably persisted as isolated subunits near springheads. Periods of high spring flow and low-level flooding would have created new aquatic habitats and permitted migration between ciénegas. Clearly, the plight of these fishes today results from reduced spring flow and fewer migration opportunities, both of which have been eliminated by the development of the irrigation system.

The greatest threat for the long-term survival of *C. elegans* is hybridization with *Cyprinodon variegatus* (sheepshead minnow), which is known to occur in the Lake Balmorhea system (Stevenson & Buchanan 1973; Echelle et al. 1987; Echelle & Echelle 1994). More than two decades of contact between introduced *C. variegatus* and *C. elegans* at Lake Balmorhea has resulted in 5% F₁ hybrids and 3% backcross progeny in that population (Echelle & Echelle 1994). Although fertility of F₁ hybrids appears to be low (males may be sterile, but females often had ripe eggs) and genetic introgression is fairly limited at this location, *C. variegatus* vastly outnumber *C. elegans*, so that the frequency of interspecific matings by *C. elegans* is likely to be high. When compared with other desert pupfishes (e.g., *C. pecosensis*), *C. elegans* at Lake Balmorhea show relatively low genetic introgression with *C. variegatus* (Echelle & Echelle 1994). However, even low levels of introgression may pose a serious threat to the long-term viability of this endemic species. Because we lack data on fish movement into the refuge, we cannot assess the suitability of the Phantom Lake Spring refuge as a safeguard against future genetic contamination from *C. variegatus* or other introduced congeners. Because it is located 6 km from the larger populations inhabiting the canals, pool, and new constructed ciénega at the state park, it seems likely that a persistent *C. elegans* population situated near the spring outflow serves as a good safeguard against the threat of genetic introgression from exotic congeners.

As already noted, both *C. elegans* and *G. nobilis* are opportunistic fishes with great capacity for rapid population growth in suitable habitats, and this was clearly demonstrated by their population dynamics during the first year after stocking of a small number of individuals of each species. In its current condition, the habitat within the refuge appears to be more suitable for *G. nobilis* than *C. elegans*. In fact, the abundance of *C. elegans* peaked after approximately one year and declined as aquatic vegetation continued to eliminate open water

areas within the refuge. Dense vegetation without patches of open substrate for spawning may be detrimental for *C. elegans*. With respect to the interaction between *G. nobilis* and *G. geiseri*, the situation in the refuge seems to be different than in the canals of Balmorhea State Park, where *G. geiseri* is reported to be gradually replacing *G. nobilis* (Echelle & Echelle 1980; Hubbs et al. 1995). Hubbs et al. (1995) noted that *G. geiseri* dominates open water habitats and *G. nobilis* dominates vegetated areas within the canals. This observation is consistent with our finding that *G. nobilis* density greatly increased while *G. geiseri* densities remained very low during vegetational succession in the refuge.

Endangered Species: Are Artificial Refuges the Solution?

The channel refuge was constructed at Phantom Lake Springs to achieve a compromise solution that (1) increases the odds for the long-term survival of two endangered fishes while (2) having minimal impact on the distribution of spring discharge to users of the Reeves County Water Improvement District. Motivation for achieving the latter goal is clear. The local economy is heavily dependent on irrigation water from Phantom Lake Springs, San Solomon Springs, and the underground aquifer from which they are derived. From the Bureau of Reclamation's standpoint, the motivation for achieving the former goal was compliance with the ESA. The ESA was created with three basic objectives (Section 2[b]): (1) to conserve the ecosystems upon which endangered species and threatened species depend; (2) to conserve such endangered and threatened species; and (3) to help achieve the purposes of a list of treaties and conventions (Section 2[a]). Results from our two year survey of the refuge indicate that the refuge likely will increase the odds for the long-term survival of the two endangered fishes.

A major impetus for enacting the ESA was that endangered species serve as warning signals that humans are altering the earth's biosphere in ways that are irreversible and potentially detrimental for ecosystem integrity and sustainability. For the vast majority of endangered species, the political and scientific debate is centered squarely on the determination of the amount of critical habitat required for maximizing the long-term survival of rare species (i.e., the objective of ecosystem conservation). If the primary objective were merely to preserve the integrity of species' genomes for all time, then aquarium, zoo, and herbarium breeding programs would be the most secure and cost-effective means to achieve that goal in many cases. For example, uncontaminated stocks of *C. elegans* and other small fishes of the southwestern United States are currently maintained at several federal fish hatcheries. Small fishes with opportunistic-type life history strategies,

such as *Cyprinodon* spp. and *Gambusia* spp., can be propagated in captivity with relative ease. If our only goal were to simply maintain species' genomes into perpetuity, then the refuge at Phantom Lake Spring probably is unnecessary, given the fact that stocks can be maintained in hatcheries (although this is not without risks, see Hubbs & Jensen 1984). If a major objective were to preserve an amount of natural habitat that ensures the long-term survival of the rare species, then the refuge probably falls short of the mark, because it does not restore the fishes' historical habitat, the ciénegas of Comanche Springs and the Toyahvale Creek basin.

Is the Phantom Lake Spring refuge a halfway technology for endangered species conservation in the sense discussed by Meffe (1992)? In one sense, the refuge is a hatchery raceway containing simulated natural aquatic habitat that is located at the geographic coordinates of one of the species' important historic habitats. This historic habitat, the ciénega, no longer exists, because virtually all of the spring's outflow is now directed to the Water District's irrigation canals. Because it was designed specifically for the endangered fishes and not for invertebrates, wildlife, and plants, only one of the ecosystem functions performed by the ciénega are performed by the constructed refuge. In some respects, the refuge channel probably functions like a segment of the historic ciénega. However, the natural habitat dynamics resulting from discharge variation and interactions with the underlying sediments are probably very different, due to the young age of the system. Ciénegas are considered to be climax communities (Hendrickson & Minckley 1984), in which cattails are occasionally present but never dominant (Bolen 1964; Hendrickson & Minckley 1984).

The irrigation system has also become firmly entrenched as the status quo, and few people would reasonably argue for cutting off any significant portion of the local community's lifeblood. Even though the political-social-economic climate of the region is unlikely to change in the foreseeable future, compromises have been made and the refuge channel represents an initial step. A cooperative effort among several state and federal agencies and citizen groups has created a restored ciénega habitat in the Balmorhea State Park in Reeves County. Though perhaps more vulnerable to introductions of nonindigenous species than the Phantom Lake Spring refuge, in our opinion, this restored ciénega comes much closer to the goal of conservation of the ecosystems that support endangered species.

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