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Use of restored floodplains by fishes of the Middle Rio Grande, New Mexico, USA

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Abstract

Nearly 1600 ha of habitat have been restored at 300 floodplain sites of the Middle Rio Grande (MRG), New Mexico, USA, as part of a cooperative effort of the Middle Rio Grande Endangered Species Collaborative Program to conserve the endangered Rio Grande silvery minnow (RGSM). These riverside sites are designed to inundate during spring run-off and create ephemeral habitats for other aquatic and riparian species. This study of four restored floodplain sites in May–June 2017 found that of 14 fish species captured with fyke nets, common carp (41%), red shiner (32%), RGSM (16%) and white sucker (9%) dominated total numbers. Adult RGSM included 42% gravid females, 36% ripe males and 22% spent females, suggesting that this endangered species was spawning in and near these floodplains. Larval sampling also showed that restored sites and adjacent mainstem banklines were being used as nursery habitats, where RGSM larvae dominated six and nine species with 80% and 74% of total numbers, respectively. System-wide proportions of RGSM larvae by phase suggest that larvae leave the floodplains and move to mainstem banklines beginning as late mesolarvae and metalarvae (14–22 days post-hatch), and most depart by the juvenile stage. Altogether, 15 fish species were encountered in restored floodplain sites in 2017, compared to 16 species reported in concurrent annual mainstem monitoring. This study and others show that most fish species of the MRG move onto restored and natural floodplains equally in spring, and many use these habitats for spawning and as larval nurseries.

KEYWORDS

habitat, larvae, mainstem banklines, Middle Rio Grande, pelagophils, restored floodplains, Rio Grande silvery minnow

1 | INTRODUCTION

The signatories of the Middle Rio Grande Endangered Species Collaborative Program (MRGESCP) have made considerable investments into restoring and rehabilitating riparian and riverine habitats of the Middle Rio Grande (MRG) in New Mexico. About 300 floodplain sites have been constructed since 2003 to inundate at low and moderate spring flows and to restore floodplain connection and enhance riparian and aquatic habitats. The efficacy of these activities continues to be evaluated for riparian vegetation, birds, mammals and fish (Caplan & McKenna, 2019; McKenna, Caplan, & Widener, 2020; Tetra Tech, Inc., 2004, 2014), including the federally endangered Rio Grande silvery minnow (RGSM, *Hybognathus amarus*), an endemic species of the Rio Grande.

The RGSM is a small (<100 mm long), short-lived, schooling cyprinid that spawns primarily in the spring by releasing and fertilizing eggs in the water column that remain semi-buoyant and hatch as altricial larvae, ~4 mm long, in 2–4 days. It is hypothesized that the eggs and larvae are pelagic and are transported long distances downstream with an upstream return of young to natal areas (Dudley & Platania, 2007). Alternatively, the species is thought to be primarily a demersal floodplain spawner with evolved secondarily buoyant eggs in high-sediment environments, and the observed long-distance drift is an artefact of channelization and contemporary flow management that has led to reduced lateral connectivity and delinking of the floodplain (Medley & Shirey, 2013). This ecological artefact and the strong relationship between high spring discharge and October catch per unit effort (CPUE) (Dudley, Platania, & White, 2018; U.S. Fish and Wildlife Service [USFWS], 2016) are strong evidence that the species is floodplain dependent, but the mechanisms behind this relationship are not well understood.

In 2008, the New Mexico Interstate Stream Commission (NMISC) began a series of studies of the restored floodplain sites, describing daily trends in abundance of spawning RGSM (Gonzales, Haggerty, & Lundahl, 2012) and the use of constructed floodplain habitats by MRG fishes (Gonzales, Tave, & Haggerty, 2014). In 2016, the NMISC began the first systematic studies of larval fish in restored sites, reporting that the majority of larvae in floodplains were RGSM (Valdez, Haggerty, Richard, & Klobucar, 2019). The study described in this paper is a follow-up to the 2016 study. It describes fish use of selected restored floodplain sites, compares habitat used by RGSM in floodplains and along mainstem banklines and incorporates otolith analysis to determine hatch and spawn dates of RGSM (Zipper, Valdez, & Haggerty, 2020). These studies help to inform the relationship between spring run-off, floodplain habitat and abundance of RGSM. They also identify the principal habitat features important to ongoing floodplain restoration projects.

The Rio Grande is a principal river of the south-western United States that begins in south-central Colorado and flows south and then southeast for 3059 km to the Gulf of Mexico (Figure 1). It is the fourth longest river in the United States and bisects the state of New Mexico before forming the international boundary with Mexico along the southern Texas border (International Boundary and Water Commission, https://www.ibwc.gov/CRP/riogrande.htm). The Rio Grande through New Mexico was historically a wide, braided river that migrated laterally with expansive and variable spring flooding (Figure 2). Extensive flood control and water use, starting in the 1920s, transformed the river to a narrow channel confined by levees and jetty jacks, delinking the floodplain from the main channel (Molles, Crawford, Ellis, Valett, & Dahm, 1998). These geomorphological and hydrological changes have negatively affected many native riverine and riparian species, including the fish community.

Among the fish species most affected are the 'pelagophils' or broadcast spawners (Platania & Altenbach, 1998). These minnows

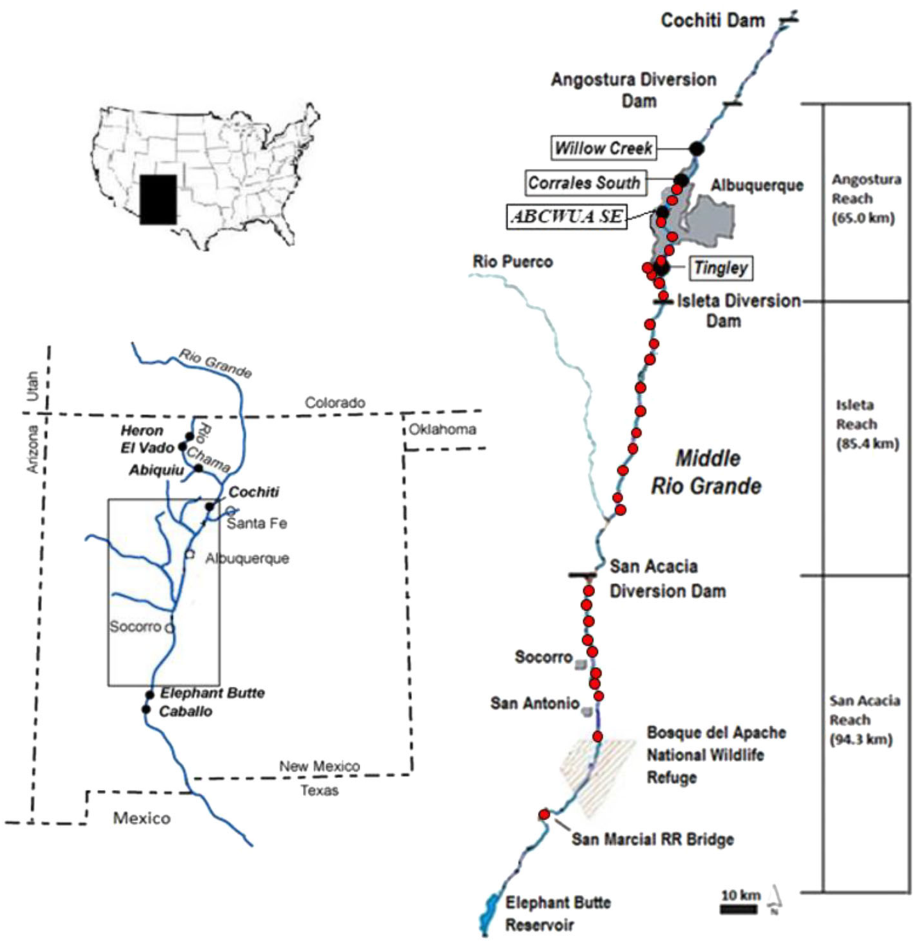

FIGURE 1 Locations of four restored floodplain sites (labelled boxes) and 30 inundated mainstem banklines locations (red dots) sampled in the Middle Rio Grande, NM, May–June 2017

FIGURE 2 The Rio Grande at Central Avenue, Albuquerque, NM, in 1933 (top) showing a wide, braided channel (reproduced with permission of the Middle Rio Grande Conservancy District) and the contemporary river (bottom) at approximately the same location showing a narrow, confined channel

maximize their reproductive success by releasing and fertilizing their eggs in the water column in response to rapidly increasing sediment-laden spring flow and water temperature (Cowley, Alleman, Sallenave, McShane, & Shirey, 2009). Of 21 fish species native to the Rio Grande in New Mexico (Propst, 1999), five have been extirpated, two are extinct and one is federally endangered, the RGSM (USFWS, 1994). The RGSM and the two extinct species (i.e., phantom shiner, *Notropis orca*, and Rio Grande bluntnose shiner, *Notropis simus simus*) relied historically on widespread floodplain formation for spawning and rearing, but these reproductive phenologies have been disrupted by the reduced frequency and magnitude of spring floodplain inundation (Krabbenhoft, Platania, & Turner, 2014; Turner, Krabbenhoft, & Burdett, 2010). The RGSM is now found in only about 5% of its original range, with the only remaining wild population in 280 km of the MRG between Cochiti Dam and Elephant Butte Reservoir, New Mexico (Bestgen & Platania, 1991), which is the area where this study was conducted (Figure 1).

The loss of riparian and floodplain habitat in the MRG has brought attention to the relationship between river discharge and floodplain formation, and in 2003, the USFWS issued a biological opinion (USFWS, 2003) that directed federal agencies '… to increase backwaters and oxbows, widen the river channel, and/or lower river banks to produce shallow water habitats, over-bank flooding … to benefit the Rio Grande silvery minnow'. A second biological opinion in 2016 (USFWS, 2016) further identified large-scale habitat restoration and conservation storage of water for release to inundate these habitats, as two of four key conservation needs for a RGSM recovery and survival strategy. These directives were intended to enhance floodplain inundation by restoring and reconnecting the low-lying riverside areas of the MRG.

Starting in 2003, the MRGESCP (https://webapps.usgs.gov/MRGESCP/index.html) created or restored nearly 1600 ha of habitat under a water depletion-neutral framework that mechanically modified banklines, islands and old floodplains to create backwaters, embayments, terraces and depressions that would inundate at discharges of 1500 ft^3/s (42.5 m^3/s) to 3500 ft^3/s (99.1 m^3/s) (Tetra Tech, Inc., 2004). About 300 floodplain sites, 0.4–5 ha in size, have been constructed in the MRG (Figure 3). These sites are designed to become inundated during low to moderate spring run-off, provide low-velocity habitat for fish during high river discharge, and entrain eggs and larvae for rearing.

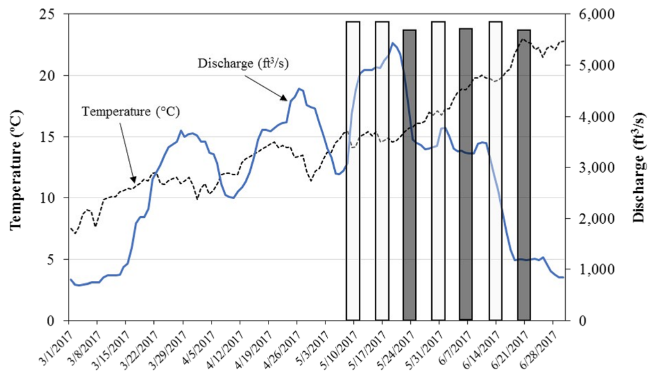

FIGURE 4 Mean daily discharge and temperature of the Middle Rio Grande at the Alameda Bridge (USGS 08329918) before and during sampling periods of restored floodplain sites (light vertical bars) and inundated mainstem banklines (dark vertical bars)
May–June 2017

2 | METHODS

2.1 | Sampling restored floodplain sites

Four restored floodplain sites were sampled in the Angostura Reach of the MRG during 8 May to 21 June 2017, including Willow Creek (RM 201.5 [river miles upstream from Elephant Butte Dam]), Corrales South (RM 193.1), ABCWUA SE (RM 190.5) and Tingley (RM 183.0) (Figure 1). The four sites were each sampled during four 4-day periods, with 4- to 10-day increments. Sampling took place during the third of three flow spikes that peaked in late March, late April and mid-May (Figure 4). All four sites remained inundated during sampling, and at highest discharge, restored floodplains and mainstem banklines sometimes became a continuous area of mostly inundated riparian vegetation.

Floodplains were sampled daily with fyke nets and larval dip nets. Fyke nets consisted of a D-frame 2.1 m long × 1.0 m wide × 0.60 m high, and double wings each 4.6 m long × 0.6 m high, and a 5-cm-diameter throat, all fitted with 3.1-mm Delta mesh. Each net was held in place with 1-m metal posts. One fyke net was set each at the inlet, centre and outlet of each site in the morning and retrieved approximately 3 to 6 h later. Total numbers of fyke nets set were Willow Creek (45), Corrales South (45), ABCWUA SE (47) and Tingley (47).

After the fyke nets were set, dip nets were used to collect larvae with a standardized 1-m sweep. Each dip net had a 1-m handle attached to a D-frame hoop 30 × 20 cm with 243-μm Nitex mesh. Dip net samples were taken at 50 randomly selected locations at each site that were kept consistent throughout the study. The 50 locations were randomly split into two groups, such that 25 dip net samples were taken the first day of sampling at each site and the remaining 25 samples on the following day. This was repeated until all

FIGURE 3 Amphibious caterpillar excavating a floodplain (upper left, SWCA), a terraced bankline (lower left, SWCA) and the Corrales floodplain site (right, Todd Caplan), all on the Middle Rio Grande, NM

50 locations were sampled twice in a 4-day period for a potential of 100 dip net locations at each site. Total numbers of dip net samples were Willow Creek (372), Corrales South (291), ABCWUA SE (330) and Tingley (270).

Habitat variables were measured at each dip net location. Water depth and distance to water's edge (i.e., nearest land–water interface) were measured with a graduated wading rod, velocity with a Global Water Flow Probe (model FP111) and temperature with a Hanna pHEP meter (model HI 98127). Per cent of in-water cover was estimated visually, and overhead canopy was measured with a 17-point spherical convex densitometer as a single measurement taken in the middle of each dip net sweep immediately above the water surface. For cover type, terrestrial woody vegetation included cottonwood (*Populus* spp.), Russian olive (*Elaeagnus angustifolia*), salt cedar (*Tamarix* spp.) and willow (*Salix* spp.). Terrestrial herbaceous vegetation included grasses and rooted vegetation. Aquatic vegetation was not encountered in the restored sites. Dominant substrate types were classified according to the Wentworth scale (Wentworth, 1922) but were principally sand and silt.

2.2 | Sampling mainstem banklines

Mainstem banklines were sampled 22 May to 21 June 2017, with the same dip net technique and the habitat measurements described previously. Fyke nets were not used along banklines. Thirty mainstem locations were randomly selected in 197 km of the MRG (RM 190.85 to 68.49, Figure 1), including 10 in each of the three reaches (i.e., Angostura, Isleta and San Acacia). A minimum distance of 500 m was maintained between sample locations to ensure sample independence. Prior to sampling, a 30-m transect was delineated at each location parallel to the channel edge. Dip net samples were taken at 20 points along the 30-m transect at each of the 30 sampling locations during each of three 4-day sample periods (Figure 4). Changing river levels caused us to move some sampling locations laterally or perpendicular to ensure that samples were taken in inundated habitat, a total of 1800 dip net samples were taken from inundated mainstem banklines.

2.3 | Processing samples

Fish captured in fyke nets were identified to species, counted and released on-site. The first 30 RGSM in each net were measured for standard length (SL), weighed in grams, assessed for reproductive condition (i.e., ripe, gravid, spent or unknown), checked for visible implant elastomer (VIE) tags used by other studies, photographed and released. Females and males were identified through expression of eggs or milt. The RGSM in excess of 30 individuals were measured, counted and released to reduce handling stress. The CPUE for each fyke net was calculated as the total number of fish captured by species divided by the total number of hours set (Gonzales et al., 2012).

The larval fishes of each dip net were placed in individual labelled plastic vials with 95% ethanol and transferred to a laboratory for enumeration and identification. In the lab, each RGSM was identified and measured to the nearest 0.1 mm, and the ontogenetic developmental phase was determined as protolarvae, flexion mesolarvae, postflexion mesolarvae, metalarvae or juvenile (Brandenburg, Snyder, Platania, & Bestgen, 2018). All larval fish were identified to species, enumerated and assessed at the Museum of Southwestern Biology, University of New Mexico, Albuquerque.

2.4 | Data recording and analysis

All field data were recorded on-site on a Samsung tablet with Open Data Kit software and GPS capability and uploaded nightly to a secure database. Data were stored and organized on an Access platform and analysed with the statistical program R (R Core Team, 2017), including the R packages: 'logistf' (Heinze & Ploner, 2016), 'MASS' (Venables & Ripley, 2002), 'PerformanceAnalytics' (Peterson, 2019), 'piscl' (Jackman, 2017) and 'vegan' (Oksanen et al., 2019).

The hatch date of each larval RGSM was estimated from fish length using a relationship developed by Zipper et al. (2020) from daily otolith increments of RGSM larvae collected from the MRG in 2017 as daily age = −15.7 + (0.565 * temperature of capture) + (2.95 * SL). Daily age (days post-hatch, dph) was subtracted from the collection date to determine the date of hatching for each fish, and the date of spawning was assumed to be 2 days earlier (Platania & Dudley, 2003).

3 | RESULTS

3.1 | Fish in restored floodplains

Altogether, 6611 fish comprising 14 species were caught with fyke nets in the four restored floodplain sites (Table 1). The most abundant species were common carp (41% of total number), red shiner (32%), RGSM (16%) and white sucker (9%). The remaining 10 species each comprised <1% of total catch. The site with the largest number of fish captured was Corrales South (3049), with 82% of total catch as common carp, followed by Tingley (2208) with 46% red shiner, 29% RGSM and 17% white sucker (Table 2). The largest numbers and CPUEs for RGSM captured with fyke nets were at Tingley (635, 2.21) and Corrales South (206, 0.67).

Of 1041 RGSM captured with fyke nets, 618 were measured for a mean length of 53.5-mm SL (range, 23–87 mm). Modal progression analysis (i.e., Bhattacharya's method, Bhattacharya, 1967; Sparre & Venema, 1998) of length histograms from three of the four sample periods revealed up to four size groups (Figure 5), with a dominant size of 40- to 60-mm SL, which were the presumed Age 1 fish (2016 year class [yc]). There appear to be Age 2 (55- to 67-mm SL), Age 3 (71- to 81-mm SL) and Age 4 (75- to 87-mm SL) fish present as

TABLE 1 Number and per cent of fish by species captured with fyke nets and dip nets in restored floodplain sites and inundated mainstem banklines of the Middle Rio Grande, May–June 2017

		Restored floodplains				Mainstem banklines	
		Fyke nets		Dip nets		Dip nets	
Species	Species code	No.	Per cent	No.	Per cent	No.	Per cent
Blue catfish, *Ictalurus furcatus*[a]	ICTFUR	1	0.02	0	0.00	0	0.00
Channel catfish, *Ictalurus punctatus*	ICTPUN	9	0.14	0	0.00	0	0.00
Common carp, *Cyprinus carpio*	CYPCAR	2710	40.99	14	2.13	3	0.13
Fathead minnow, *Pimephales promelas*[a]	PIMPRO	18	0.27	29	4.41	186	7.83
Flathead catfish, *Pylodictis olivaris*[a]	PYLOLI	3	0.05	0	0.00	0	0.00
Flathead chub, *Platygobio gracilis*[a]	PLAGRA	38	0.57	0	0.00	2	0.08
Green sunfish, *Lepomis cyanellus*	LEPCYA	9	0.14	0	0.00	0	0.00
Largemouth bass, *Micropterus salmoides*	MICSAL	1	0.02	0	0.00	0	0.00
Longnose dace, *Rhinichthys cataractae*[a]	RHICAT	6	0.09	0	0.00	2	0.08
Red shiner, *Cyprinella lutrensis*[a]	CYPLUT	2146	32.46	0	0.00	4	0.17
Rio Grande silvery minnow, *Hybognathus amarus*[a]	HYBAMA	1041	15.75	526	80.06	2141	90.15
River carpsucker, *Carpiodes carpio*[a]	CARCAR	0	0.00	1	0.15	0	0.00
Smallmouth buffalo, *Ictiobus bubalus*[a]	ICTBUB	0	0.00	0	0.00	3	0.13
Western mosquitofish, *Gambusia affinis*	GAMAFF	26	0.39	1	0.15	5	0.21
White crappie, *Pomoxis annularis*	POMANN	1	0.02	0	0.00	0	0.00
White sucker, *Catostomus commersonii*	CATCOM	602	9.11	86	13.09	29	1.22
Total		6611	100.00	657	100.00	2375	100.00

Note: Fish captured with fyke nets were larger, non-larval fishes. Fish captured with dip nets were larvae and small juveniles. Species codes are the first three letters of the genus and species.
[a]Native species (Propst, 1999).

TABLE 2 Number of fish by species captured with fyke nets in each of four restored floodplain sites of the Middle Rio Grande, 8 May to 21 June 2017

Common name	Willow Creek	Corrales South	ABCWUA SE	Tingley	Total	Per cent
Common carp	78	2492	16	124	2710	40.99
Red shiner	390	265	473	1018	2146	32.46
Rio Grande silvery minnow	48 (0.14 ± 0.27)	206 (0.67 ± 1.49)	152 (0.56 ± 0.84)	635 (2.21 ± 2.19)	1041 (0.84 ± 0.73)	15.75
White sucker	106	65	53	378	602	9.11
Flathead chub	0	2	18	18	38	0.57
Western mosquitofish	10	11	2	3	26	0.39
Fathead minnow	3	3	0	12	18	0.27
Channel catfish	0	0	1	8	9	0.14
Green sunfish	0	1	0	8	9	0.14
Longnose dace	3	3	0	0	6	0.09
Flathead catfish	0	0	0	3	3	0.05
Blue catfish	0	0	0	1	1	0.02
Largemouth bass	0	1	0	0	1	0.02
White crappie	1	0	0	0	1	0.02
Total	639	3049	715	2208	6611	100.00

Note: CPUE ± standard error is shown for RGSM.

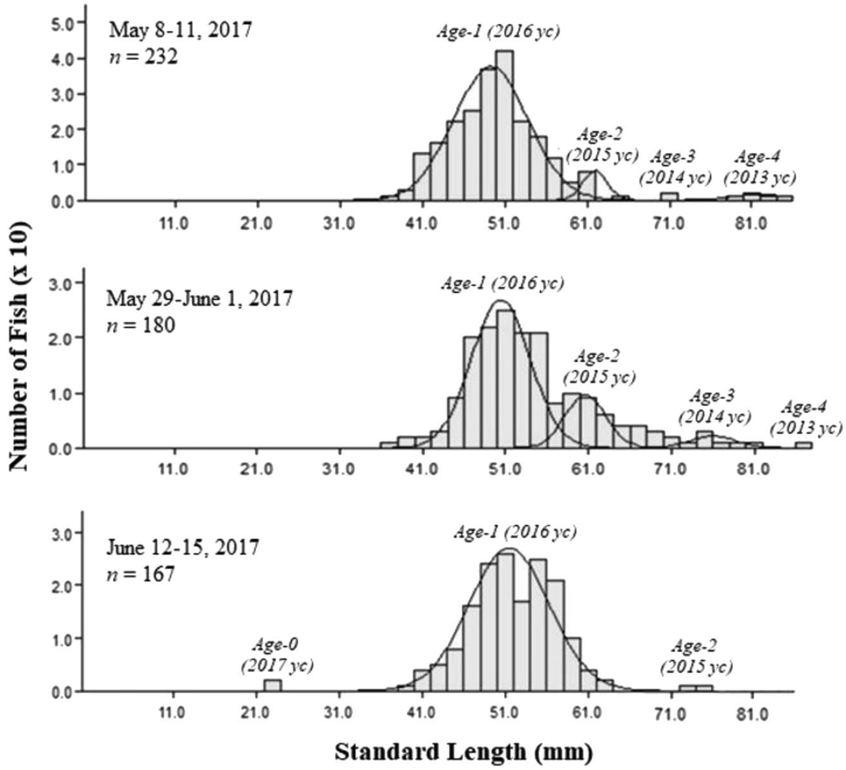

FIGURE 5 Length modes (2-mm increments) and presumed ages and year classes (yc) of Rio Grande silvery minnow captured with fyke nets from four restored floodplain sites of the Middle Rio Grande, NM, May–June 2017. Smooth lines show most probable modes using Bhattacharya's method

represented by apparent smaller modes, and two individuals of Age 0 (2017 yc) appeared in the last sample period as 23-mm SL. Age 0 fish were hatching or in the larval stage during these sample periods, and most were too small to catch in fyke nets. Reproductive condition of 292 RGSM showed that 123 (42%) were gravid females, 106 (36%) were ripe males and 63 (22%) were spent females. These fish were apparent age-1 and age-2+ fish.

Movements of RGSM to and from the four restored sites were not detectable from individually placed fyke nets (i.e., inflow vs. outflow), but the daily CPUE of fish in all three nets appeared to be related to changes in river discharge. Highest CPUEs of 6.7 fish/h at Tingley and 6.1 fish/h at Corrales were simultaneously observed for the sample period 8–11 May, which occurred concurrent with a 1750-ft^3/s (49.6 m^3/s) increase in discharge (3090 ft^3/s [87.5 m^3/s] to 4840 ft^3/s [137.1 m^3/s]) of the Rio Grande at Albuquerque (USGS 08330000). High CPUE was not seen for the second sample period 15–18 May when discharge was high and relatively stable at 4960 ft^3/s (140.5 m^3/s) to 5190 ft^3/s (147.0 m^3/s) (230-ft^3/s increase). A second period of high CPUEs was observed at the Tingley site 29 May to 1 June, when discharge increased 390 ft^3/s (11.0 m^3/s), from 3390 ft^3/s (96.0 m^3/s) to 3780 ft^3/s (107.1 m^3/s). A third pulse of relatively high CPUE took place at the ABCWUA SE site and the Tingley site during 12–15 June, when flow decreased by 1060 ft^3/s (30.0 m^3/s), from 3200 ft^3/s (90.6 m^3/s) to 2140 ft^3/s (60.6 m^3/s).

Altogether, 657 larvae of six fish species were collected in the four restored sites, including 526 RGSM (80% of total number), 86 white sucker (13%), 29 fathead minnow (4%) and 14 common carp (2%) (Table 1). The remaining two species each comprised <1% of total catch (i.e., river carpsucker and western mosquitofish). The largest number and catch of RGSM larvae were at Corrales South (483, 1.78 fish per 100 m^2), despite more dip net samples taken at each of the three other sites (Table 3). Number and catch of RGSM

TABLE 3 Number and mean CPUE for Rio Grande silvery minnow larvae collected with dip nets from four restored floodplain sites of the Angostura Reach and along mainstem banklines of the Angostura, Isleta and San Acacia reaches, May–June 2017

Restored floodplains				Mainstem banklines			
Site	No. of RGSM	No. of dip nets	Mean CPUE (no. per sweep)	Reach	No. of RGSM	No. of dip nets	Mean CPUE (no. per sweep)
Willow Creek	11	370	0.03	Angostura	124	598	0.21
Corrales South	483	271	1.78	Isleta	1701	596	2.85
ABCWUA SE	21	335	0.06	San Acacia	316	556	0.57
Tingley	11	281	0.04	—	—	—	—
Total	526	1257	0.42	Total	2141	1750	1.22

larvae at the other sites were ABCWUA SE (21, 0.06 fish per 100 m^2), Willow Creek (11, 0.03) and Tingley (11, 0.04).

3.2 | Larval fishes along mainstem banklines

Altogether, 2375 larval fish of nine species were collected from 30 mainstem bankline locations of the Angostura, Isleta and San Acacia reaches (Table 1). The most abundant species were RGSM (2141, 90%), fathead minnow (186, 8%), white sucker (29, 1%) and common carp (3, <1%). This was a similar larval fish composition as seen in the four restored floodplain sites of the Angostura Reach with RGSM (526, 80%), white sucker (86, 13%), fathead minnow (29, 4%) and common carp (14, 2%). The largest number and CPUE of RGSM larvae were collected in the Isleta Reach (1701, 2.85), followed by the San Acacia Reach (316, 0.57) and the Angostura Reach (124, 0.21) (Table 3).

3.3 | Developmental phases of RGSM larvae

All four phases of RGSM larvae were collected in restored floodplain sites, including 9 protolarvae, 179 flexion mesolarvae, 95 postflexion mesolarvae and 239 metalarvae, as well as 4 juveniles. The proportions of these developmental phases at all sites for the four sample periods are shown in Figure 6. Protolarvae were not abundant during the first sample period, suggesting that either spawning had not occurred in the sites or spawning had occurred before sampling began and the larvae had already transitioned to mesolarvae. The flexion and postflexion mesolarvae were predominant and persisted midway through the third sample period to about 1 June. The metalarval phase first appeared about 29 May and increased in proportion to the end of the study. The reappearance of protolarvae on 1 June suggests a second spawning event concurrent with the flow increase of 29 May to 1 June and the increased daily CPUE of adult RGSM. A notable decline in the proportion of all developmental phases occurred by the fourth sample period, indicating the end of spawning. Only four juveniles were collected altogether from restored floodplain sites.

As with the RGSM larvae collected in the four restored sites, the larvae from the mainstem were classified by developmental phase for each of the three sample periods (Figure 6). The 2122 RGSM larvae from mainstem banklines included 1167 protolarvae, 147 flexion mesolarvae, 241 postflexion mesolarvae, 383 metalarvae and 184 juveniles. The transition of larval phases is evident from the proportions of phases for the three sample periods. Protolarvae were captured only during the first period (22–25 May), suggesting that

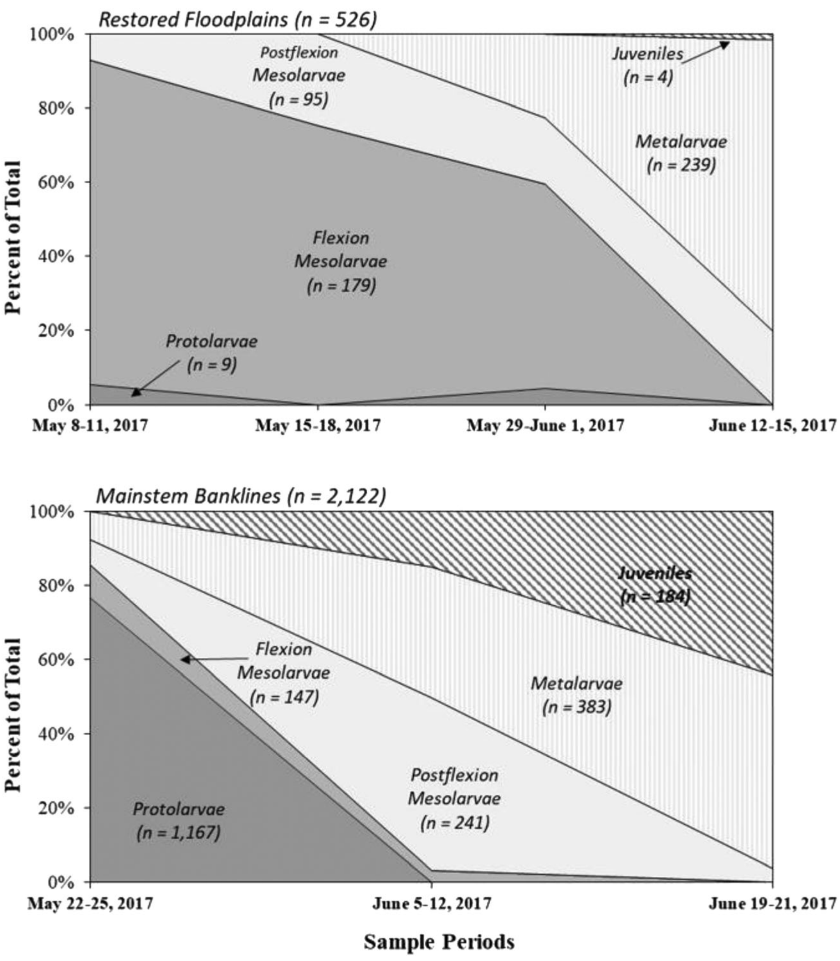

FIGURE 6 Proportions of larval Rio Grande silvery minnow by developmental phase from four restored floodplain sites and 30 mainstem bankline locations, computed as the sum of daily samples for each of the indicated sample periods. Note that the sample periods for the two graphs differ

mainstem spawning had occurred prior to the sample period. The numbers of flexion mesolarvae were small, and all were caught in the first and second sample periods. The larger numbers of postflexion mesolarvae were collected late in the first sample period and through the second period, whereas metalarvae and juveniles increased in proportion through the second and third periods (early to mid-June). The greater number of juveniles along mainstem banklines was in contrast to the very low number of juveniles in the restored floodplain sites. Larvae from the mainstem Angostura Reach showed a pattern of larval phase transition similar to that of all three reaches but for a smaller sample size, and the larvae of all reaches were pooled for this analysis.

3.4 | Hatch and spawn dates of RGSM

First and last estimated hatching dates for larval RGSM were similar for restored sites (4/14 and 5/28) and mainstem banklines (4/17 and 5/29) but with significantly different distributions (two-tailed Kolmogorov–Smirnov statistic = 0.38, p < 0.001) (Figure 7). Hatching along banklines peaked 11–12 May with a larger peak than floodplains where hatching peaked 18 May. Two modes of hatched larvae were apparent each for floodplain sites and for mainstem banklines that corresponded to flow pulses, suggesting that spawning took place in response to flow increases. The second and largest mode of hatched larvae from banklines occurred earlier than the second mode for floodplains, suggesting that spawning took place along banklines about 7 days earlier than in floodplains. The timing of spawning and hatching in floodplains and banklines may be confounded by the different reach locations for the samples and by the temporary merging of the two habitats at the highest river discharges.

The distributions of hatched larvae in floodplains and banklines were similarly skewed towards a lower and early spawn concurrent with a second flow spike from mid-April to late April. These distributions suggest that hatching began simultaneously in floodplains and banklines in mid-April, remained at a low level until early May, then increased sharply in banklines concurrent with a third flow pulse, followed by another hatching event in floodplains that ended in late May. Assuming an incubation period of 2 days, the earliest estimated spawn date from floodplains in 2017 was 12 April, and the earliest estimated spawn date from banklines was 15 April (Table 4). Estimated spawn dates from banklines indicate that earliest spawning likely occurred in the San Acacia Reach (15 April), followed by the Isleta Reach (17 April) and the Angostura Reach (25 April). Based on the largest number of larvae hatched per day along banklines of the Isleta and San Acacia reaches, the assumed peak spawn dates in 2017 were 8–10 May, and the end of spawning was 26–27 May. Peak spawning in restored sites of the Angostura Reach occurred about the same time (10 May) but was over 2 weeks later (26 May) in the mainstem. Estimated spawn dates for 2016 (Valdez et al., 2019) are provided on Table 4 for comparison and are discussed later in this paper.

Cumulative temperature degree days (ACDDs) were computed from the cumulative sum of the mean daily river temperature above 5°C, starting 1 January 2017, as an index of spawning time by RGSM. Mean daily temperature of the Rio Grande at the Alameda Bridge for the earliest spawn dates of 12 April and 23 April were 12.9°C and 14.1°C, and ACDDs were 777 and 931, although the latter mainstem sample for the Angostura Reach is based on a relatively small number of larvae (92) compared to the mainstem (476) and may not accurately reflect spawn dates of fish in that area.

3.5 | Habitat associations

Habitat variables were recorded for 657 dip net locations with larvae in four restored floodplain sites. Of six species encountered, only one river carpsucker and one western mosquitofish were collected, and these species were excluded from further analyses. Larvae of the remaining four species (common carp, fathead minnow, RGSM and white sucker) were found at average depths of 13.2 to 17.4 cm, velocities of 0.0 to 4.7 cm/s, distance to water's edge of 6 to 20 m and temperatures of 17.8°C to 21.8°C (Figure 8). Only the white sucker was collected in significantly deeper, faster and cooler water. The four species were associated with 25% to 42% cover that

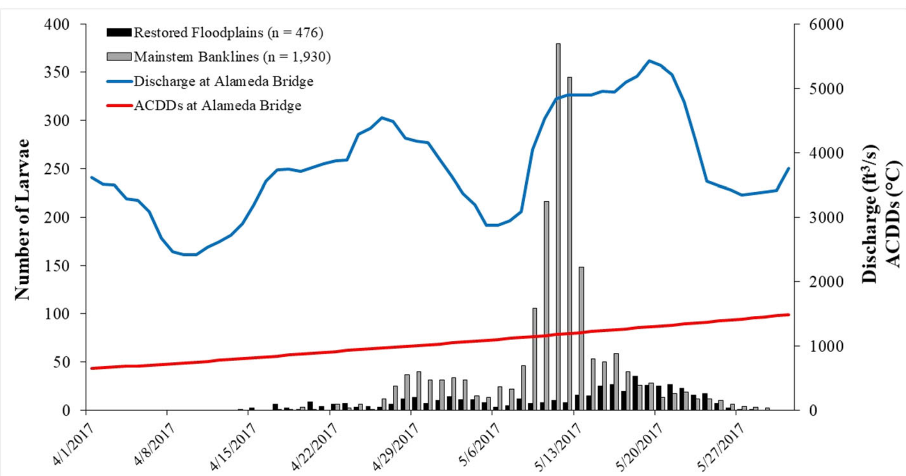

FIGURE 7 Estimated hatch dates of Rio Grande silvery minnow from restored floodplain sites and mainstem banklines, as well as river discharge and cumulative degree days (ACDDs) above 5°C for 2017. Mean daily discharge and temperature are for the Rio Grande at the Alameda Bridge (USGS #08329918)

TABLE 4 Estimated spawn dates of Rio Grande silvery minnow by reach and temperature at the Alameda Bridge for 2016 and 2017

	No. of larvae	Earliest date	Peak date	Lastest date	Earliest temp.	Earliest ACDDs
Reach (2016)						
Angostura (RFS)	1725	9 April	9 May	1 June	12.5°C	717
Isleta (RFS)	113	7 April	3 May	15 May	12.5°C	692
San Acacia (RFS)	—	—	—	—	—	—
Reach (2017)						
Angostura (RFS)	476	12 April	10 May	26 May	12.9°C	777
Angostura (IMB)	92	23 April	6 May	29 May	14.1°C	931
Isleta (IMB)	1534	17 April	10 May	28 May	14.0°C	845
San Acacia (IMB)	304	15 April	8 May	25 May	13.6°C	817

Note: Estimated spawn dates are 2 days prior to hatch dates. Numbers do not match Table 3 because accurate lengths were not available for all specimens. Estimated hatch dates were derived from a laboratory-based temperature model (Platania & Dudley, 2003; Valdez et al., 2019) for 2016 and from an otolith-based model (Zipper et al., 2020) for 2017. No significant difference was found for 2016 data recomputed with otolith-based model (two-tailed Kolmogorov–Smirnov statistic = 0.41, $p < 0.001$).
Abbreviation: ACDDs, annual cumulative degree days above 5°C.

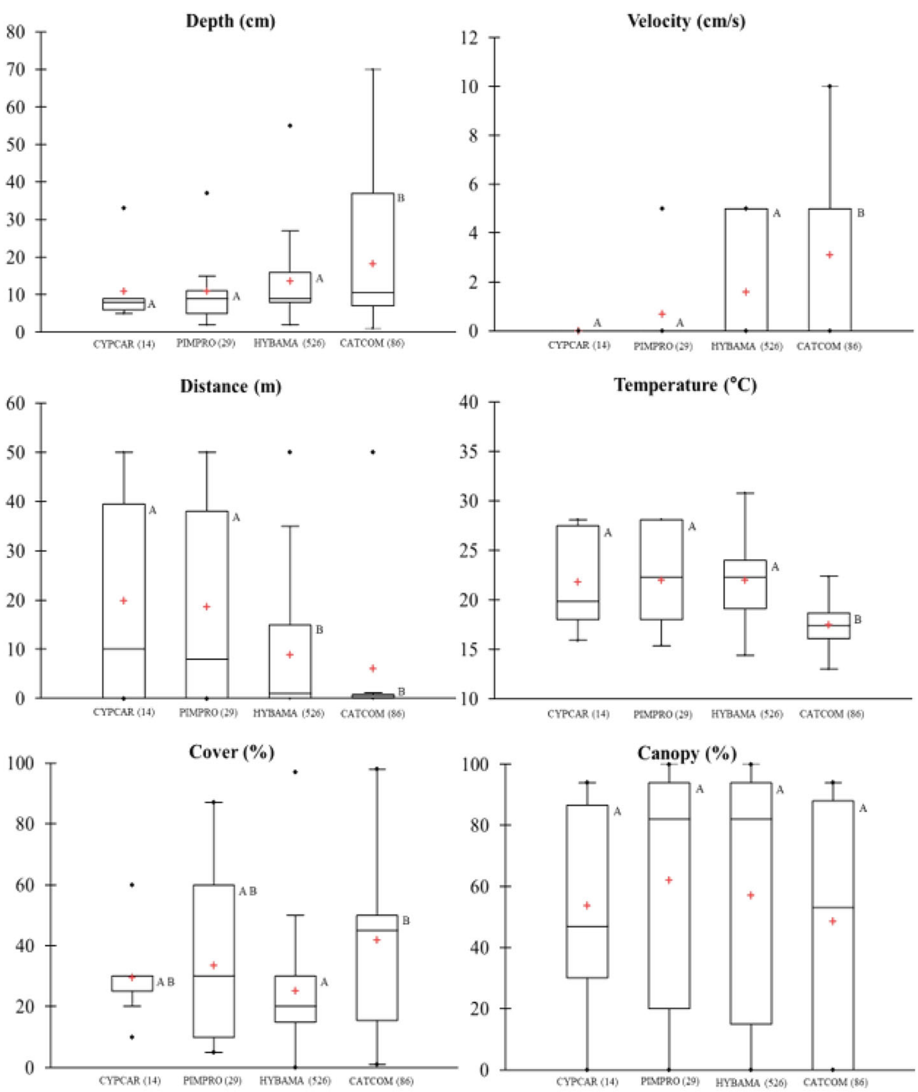

FIGURE 8 Box plots for six habitat variables of dip net locations where larval common carp (CYPCAR), fathead minnow (PIMPRO), Rio Grande silvery minnow (HYBAMA) and white sucker (CATCOM) were present in restored floodplain sites of the Middle Rio Grande. Letters A and B indicate significant differences in means (red '+') with ANOVA ($p \leq 0.05$). Dots indicate outlier values beyond interquartile range

consisted primarily of terrestrial woody and herbaceous vegetation recently inundated by spring flows. White sucker were found in similar numbers in cover as red shiner and fathead minnow but in significantly greater numbers than RGSM. Larvae of the four species were collected from locations with 6% to 62% overhead canopy, and most were associated with silt/sand substrate, the predominant substrate of the MRG (Tetra Tech, Inc., 2014).

Of nine species of larvae collected from 2359 locations along mainstem banklines, five or more specimens were collected for four species (white sucker, mosquitofish, RGSM and fathead minnow), and only these were considered in further analyses. No significant differences were found for habitat variables across reaches, and the locations with larvae were pooled for this analysis. Larvae of these species were found at average depths of 14.5 to 21.6 cm, velocities of 1.4 to 11.0 cm/s, distance to water's edge of 0.4 to 1.2 m and temperatures of 20.9°C to 27.1°C (Figure 9). Only mosquitofish were collected in significantly swifter and warmer water. Larvae of the four species were in a wide range of cover, from 6% for mosquitofish to 62% for fathead minnow that consisted primarily of recently inundated terrestrial woody and herbaceous vegetation. The larvae of all four species were collected in locations with high proportions (44% to 66%) of overhead canopy and on silt/sand substrates.

Habitat variables were evaluated for dip net locations with and without RGSM larvae, and significant differences ($p \le 0.05$) in means were tested for each variable with a one-way analysis of variance (ANOVA) and Tukey's HSD all-pairwise comparisons. Sample locations with RGSM larvae in restored floodplain sites were significantly shallower (mean = 15 cm) than those without RGSM (28 cm), as were the locations with and without larvae along inundated mainstem banklines (22 vs. 26 cm, respectively). Similarly, mean water velocity was significantly lower for locations with RGSM larvae (1 cm/s) than without (9 cm/s) in restored floodplains, as well as along mainstem banklines (6 vs. 11 cm/s, respectively).

Water temperature during sampling ranged from 13°C to 31°C, and dip net locations in restored sites had a significantly higher mean temperature with RGSM larvae (22°C) than without (18°C). Similarly, dip net locations along inundated banklines were significantly warmer with larvae (25°C) than without (23°C). The distance that RGSM larvae were found from the water's edge was measured to determine if the fish were in nearshore habitat or offshore locations. Dip net

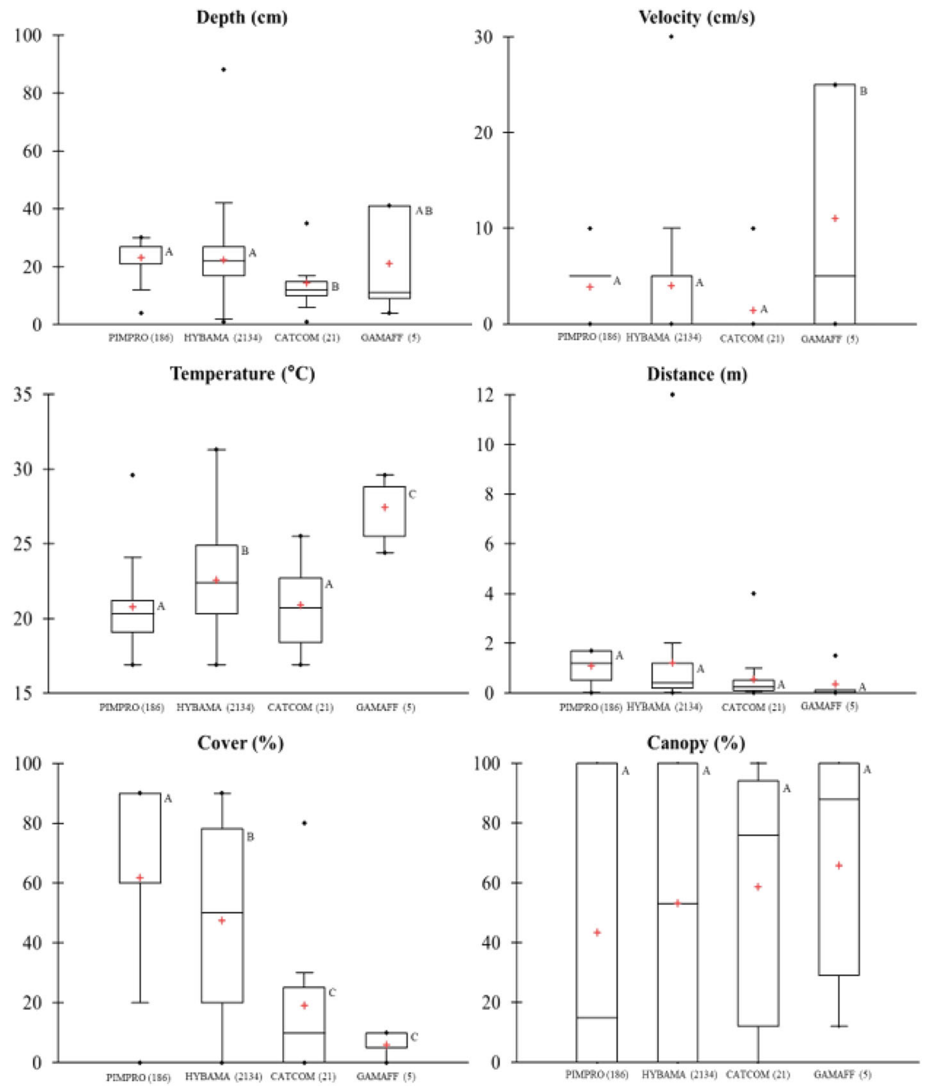

FIGURE 9 Box plots for six habitat variables of dip net locations where larval fathead minnow (PIMPRO), Rio Grande silvery minnow (HYBAMA), white sucker (CATCOM) and mosquitofish (GAMAFF) were present in mainstem banklines of the Middle Rio Grande. Letters A, B and C indicate significant differences in means (red '+') with ANOVA ($p \le 0.05$). Dots indicate outlier values beyond interquartile range

locations with larvae in restored sites were significantly closer to the water's edge (mean = 9 m) than locations without larvae (14 m), but locations with and without RGSM larvae along mainstem banklines (1.2 vs. 2.0 m, respectively) were not significantly different. Dip net samples along mainstem banklines were taken at water depth <1.4 m and velocity <1 m/s, where samples could be taken safely by wading and where larvae would not otherwise be transported downstream by river currents.

The amount of cover in the water column was not significantly different between locations with (25%) and without (24%) RGSM larvae in restored sites, indicating that cover was likely readily available. However, locations with larvae along mainstem banklines had significantly more cover (24%) than locations without larvae (15%), suggesting that RGSM larvae were using areas with the most available cover. RGSM larvae in restored sites were collected primarily in association with terrestrial herbaceous (69%) and terrestrial woody (29%) vegetation, and few were in open water (1.5%). RGSM larvae from mainstem banklines were also collected in association with terrestrial herbaceous (43%) and terrestrial woody (31%) vegetation, but some were in open water (20%). RGSM larvae were collected from locations with an average of 96% silt in restored sites and 84% silt along mainstem banklines.

The mean per cent canopy of locations with RGSM larvae (57%) was not significantly different from locations without larvae (43%) in restored floodplain sites or along inundated mainstem banklines (53% vs. 42%). Also, the large interquartile ranges for per cent canopy in restored sites and mainstem banklines suggest that canopy was associated with most habitat types, but there was no apparent selection by the RGSM larvae for areas of overhead canopy and shade.

Principal components analysis and logistic regression models were used for a more in-depth evaluation of habitat variables and their effect on the presence or absence of RGSM larvae (Figure 10). For floodplain sites, the first two factors (PC1 and PC2) explain 55% of the variability in the data. Direction and proximity of these projections and loadings (Table 5) show that temperature was strongly and positively correlated along PC1, and depth, velocity and distance were strongly correlated to each other and negatively correlated to temperature. Factor PC2 shows that cover and canopy were strongly and positively correlated, and the other factors had little influence. This factor analysis shows that in restored sites, the presence or absence of RGSM larvae was most influenced by water temperature, depth, velocity and proximity to water's edge, with vegetative cover and canopy having a lesser effect.

For inundated mainstem banklines, PC1 and PC2 explain 48% of the data variability (Figure 10). Velocity and temperature were strongly and positively correlated along PC1, and cover was strongly and negatively correlated (Table 5). Along PC2, distance to water's edge and depth were positively correlated. These correlations and the scatter of observations indicate that mainstem locations with RGSM larvae were most influenced by water velocity, temperature, depth, proximity to the water's edge and cover. Notably, canopy was highly correlated along PC3 but had less influence for RGSM larvae along inundated mainstem banklines than in floodplain sites.

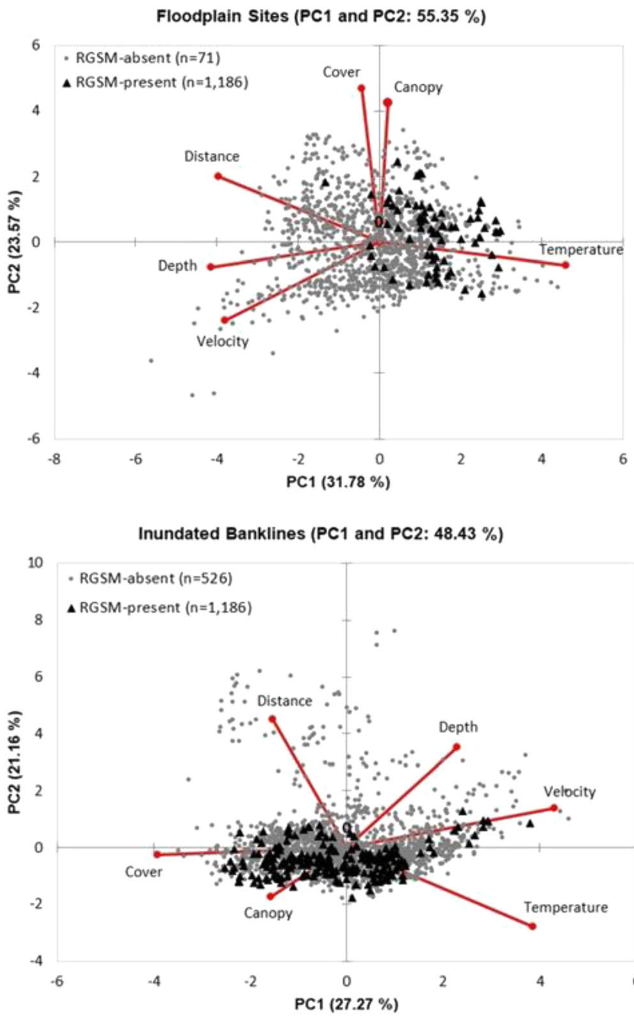

FIGURE 10 Biplots of principal component analysis for six habitat variables at dip net locations in four restored floodplain sites (top) and inundated mainstem banklines (bottom) with (present) and without (absent) Rio Grande silvery minnow larvae

4 | DISCUSSION

4.1 | Fish use of MRG floodplains

Investigations of fishes in the MRG are recent and did not occur before the extensive geomorphological and hydrological changes of the last century that transformed the river from a wide braided channel to one that is narrow and confined with little floodplain connection. Earliest reports of fishes in the MRG (Hatch, 1985; Koster, 1957; Platania, 1991; Propst, Burton, & Pridgeon, 1987; Sublette, Hatch, & Sublette, 1990) and the ongoing fish monitoring programme that began in 1993 (Dudley et al., 2018) have focused primarily on the mainstem with little attention to floodplains. Following the start of floodplain restoration in 2003, Porter and Massong (2004a) showed that newly restored floodplain sites in the MRG entrained and retained RGSM eggs as effectively as natural floodplains. In spring of 2006, Hatch and Gonzales (2008) found large concentrations of

TABLE 5 Loadings from principal component analysis of habitat variables for dip net locations from four restored floodplain sites and mainstem banklines, May–June 2017

	Restored floodplains					Mainstem banklines				
Habitat variable	**F1**	**F2**	**F3**	**F4**	**F5**	**F1**	**F2**	**F3**	**F4**	**F5**
Canopy	0.038	0.709	0.509	−0.442	0.203	−0.262	−0.291	0.807	−0.360	−0.014
Cover	−0.071	0.781	−0.484	0.060	−0.192	−0.652	−0.042	0.199	0.611	0.400
Depth	−0.691	−0.126	0.513	0.208	−0.307	0.381	0.589	0.550	0.083	0.018
Velocity	−0.630	−0.400	−0.263	−0.417	0.349	0.719	0.230	0.145	0.387	−0.036
Temperature	0.768	−0.116	0.162	0.277	0.366	0.644	−0.466	−0.022	−0.163	0.575
Distance	−0.660	0.336	−0.015	0.470	0.446	−0.257	0.753	−0.164	−0.389	0.369

Note: The higher correlated variables (>0.5), highlighted in light grey, are the variables that most affect the presence or absence of RGSM.

reproductively mature RGSM in inundated lateral overbank habitats, including floodplains, and in May–June of 2008 and 2009, Gonzales et al. (2014) reported large numbers of reproductive adult RGSM in natural and restored floodplains and concluded that spawning was likely taking place in floodplains and adjacent inundated mainstem banklines.

Fish in the contemporary MRG appear to use restored floodplains similar to natural floodplains. Gonzales et al. (2014) in spring 2008–2009 reported 15 species of fish in natural and restored floodplains, with RGSM as 80% of overall fyke net catch and red shiner only 16%. In May–June 2016, Valdez et al. (2019) caught 10 species in fyke nets that consisted primarily of red shiner (75%) and RGSM (18%), with 1% common carp and white sucker. In May–June 2017, we caught 14 species with fyke nets in four restored floodplain sites, with common carp as the most abundant species (41%), followed by red shiner (32%), RGSM (16%) and white sucker (9%). Although the same species were dominant, the relative abundances varied by year. These inter-annual variations in relative abundances of fish species in floodplains probably reflect patterns in population dynamics that are greatly influenced by annual flow regime, floodplain availability, reproductive success and survival of young.

The 15 fish species we reported as all life stages from restored sites in June 2017 are similar to the 16 species seined from the mainstem during concurrent fish population monitoring (Dudley et al., 2018). This included nearly the same list as shown in Table 1, except that gizzard shad (*Dorosoma cepedianum*), threadfin shad (*Dorosoma petenense*) and yellow bullhead (*Ameiurus natalis*) were found in the mainstem and not in the floodplains, whereas flathead catfish, green sunfish and largemouth bass were found in floodplains and not in the mainstem. Hence, a high percentage of fish species that occupy the MRG were encountered in restored floodplains in 2017, confirming that these newly constructed ephemeral habitats are used by the fish community during spring run-off.

We found a substantial proportion of adult RGSM in restored floodplains in spawning or post-spawning condition and a predominance of larvae, indicating that this endangered species is likely using the low-velocity habitats of floodplains and nearby inundated banklines for spawning, egg incubation and larval rearing. In 2017, we observed increased catches of adult RGSM in restored floodplain sites during sharp flow increases of 390–1750 ft^3/s, but not at 230 ft^3/s increase, which we interpret as spawning-related movements. Apparent spawning-related movements of adult RGSM onto natural and restored floodplains of the MRG were previously reported (Gonzales et al., 2014; Valdez et al., 2019), as well as movements into simulated floodplains for spawning in an outdoor aquaculture facility (Hutson, Toya, & Tave, 2018). Movements of fish onto floodplains during spring run-off are an observed phenomenon in other rivers, where fish seek sheltered productive habitats for thermal accumulation and gonadal maturation, spawning and feeding (Junk, Bayley, & Sparks, 1989), including the Kankakee River in Illinois (Kwak, 1988), the Mekong River in China (Baran, Van Zalinge, & Ngor Peng, 2001) and the Jamuna River in Bangladesh (de Graaf, 2003). Similar movements by other fish species are reported to natural floodplains in the Cosumnes River of central California (Moyle et al., 2007) and to reconnected floodplains of the Green River in Utah (Crowl et al., 2002).

Of the four restored floodplain sites sampled in the MRG in 2017, three were previously sampled in 2016 (i.e., Willow Creek, ABCWUA SE and Tingley; Valdez et al., 2019). Only the Corrales South site had not been sampled before. When comparing fyke net catches for similar numbers of sets in 2016 (115) and in 2017 (139), we found substantial differences in the numbers of species and individuals captured, respectively: Willow Creek (5, 99; 8, 639), ABCWUA SE (4, 226; 7, 715) and Tingley (7, 271; 11, 2208). Substantial differences were also seen for numbers of species and larvae collected with similar numbers of dip net samples in 2016 (628) and 2017 (972): Willow Creek (6, 407; 3, 21), ABCWUA SE (6, 789; 4, 48) and Tingley (6, 268; 3, 20). Differences in species and numbers of non-larval and larval fishes are likely linked to annual variation in brood stock abundance and to reproductive success and survival of eggs and larvae and make it difficult to determine which restored sites were used most by the fish. These variations are most likely driven by the dynamics of the fish populations, as well as the variability of annual river discharge, particularly in spring, and to the timing, magnitude and duration of floodplain inundation (Valdez et al., 2019).

Other aspects of these restored sites may influence the species and numbers of fish in the spring, including level of the amount of primary and secondary production, juxtaposition of the floodplain opening in the river channel, and proximity of the floodplain site to fish population centres or natural movement corridors. These and other factors need to be investigated and evaluated to better understand which restored floodplains provide the most effective habitats for fishes of the MRG, particularly the RGSM—or if the use and importance of certain floodplains sites depend on the condition of floodplains with the given hydrological regime for that year. Some restored floodplain sites may be more suitable than others in a given year because of river level and degree and timing of inundation, relative to timing of spawning and hatching of young.

4.2 | Habitat used by RGSM larvae

Floodplains of the MRG have only recently been sampled for larval fish composition. Pease, Davis, Edwards, and Turner (2006) found that inundated riverside depressions, side channels and floodplains supported a suite of species, including larvae of the endangered RGSM, highlighting for the first time the importance of these ephemeral spring habitats that were once a dominant feature of the historical river. Magaña (2012) found that RGSM used a restored floodplain site during a controlled flood pulse and also acknowledged the importance of these habitats to the larvae of RGSM. Valdez et al. (2019) evaluated habitat characteristics and timing of spawning for RGSM, found that the larvae were using shallow, low-velocity, vegetated habitats in restored floodplains and surmised that individual larvae remained in the floodplains for 14–22 dph, departing as late phase mesolarvae, metalarvae and juveniles. The study was conducted during a 2016 managed flow in the MRG and highlighted the importance of timing, magnitude and duration of spring run-off to floodplain inundation and the need for stable and persistent nursery habitat for the newly hatched larvae.

In 2017, we repeated these habitat measurements on restored floodplains and also sampled inundated mainstem banklines to compare habitat variables used by larval RGSM in different parts of the river. The larvae in restored floodplains and mainstem banklines were respectively found in shallow water (average: 15 and 22 cm), low velocity (1.2 and 4.1 cm/s), near water's edge (9 and 1.2 m), at warmest temperatures (22°C and 25°C), in vegetative cover (25% and 47%) and associated with overhead vegetative canopy (57% and 53%). The larvae occupied dip net locations similar to those of other species in floodplains and banklines, with some exceptions. As with the larvae of the other species, the biggest difference in habitat used by RGSM was the closer distance to the water's edge in floodplains and along banklines. With some exceptions, the larvae of all cyprinid species appear to use a similar range in habitat variables in restored floodplains and mainstem banklines. These findings are similar to those of Pease, Davis, Edwards, and Turner (2006) where microhabitats with lower current velocity and higher temperature appeared to be selected as nursery areas by most Rio Grande fishes and where ephemeral backwaters and disconnected side channels held the highest abundance and diversity of larvae and juveniles. Magaña (2012) also found from canonical correspondence that depth and velocity were principal habitat variables that determined fish presence in floodplains and that fathead minnow and red shiner were positively associated with depth, common carp and RGSM were positively associated with velocity and red shiner were positively associated with temperature. We report similar findings through PCA that depth, velocity and proximity to water's edge were strongly correlated with presence of RGSM larvae in floodplains and that depth, velocity, temperature, cover and distance to water's edge were strongly correlated with presence of RGSM larvae in banklines.

The biggest difference in habitat variables of RGSM larvae in floodplains versus banklines was distance from the water's edge. Dip net samples were taken 0.01- to 50-m distance in both habitats, but larvae were found up to 50 m (mean = 11.4) from the water's edge in floodplains and only up to 12 m (mean = 1 m) in banklines. The larvae were more dispersed in floodplains, whereas larvae along banklines were closer to the water's edge and away from the swifter currents of the main channel. Although mainstem banklines provide suitable habitat for larvae under certain spring flows, the suitable area may be limited to a narrow band along the shoreline, or nearly non-existent at lower and possibly highest flows, as determined primarily by velocity and velocity buffers such as vegetation. We also surmise that proximity to the water's edge is driven by the 'green bathtub ring' that provides a variety of diatoms, algae and small invertebrates as food for the young RGSM (Magaña, 2012; Watson, Sykes, & Bonner, 2009).

4.3 | Spawning locations of RGSM

Investigators have been unable to definitively determine spawning locations of wild RGSM, but recent investigations provide compelling evidence that fish are spawning in floodplains and likely on mainstem banklines where sheltered habitats minimize downstream transport of propagules (Widmer, Fluder, Kehmeier, Medley, & Valdez, 2010). Spawning has been observed in laboratory aquaria (Platania & Dudley, 2003) and in low-velocity areas of an outdoor aquaculture facility (Hutson et al., 2018), but not in the wild because high spring flow and turbid river conditions preclude direct observation of spawning fish. The high proportions of RGSM in reproductive condition and their propagules (i.e., eggs and larvae) in restored and natural floodplains and in inundated mainstem banklines (Gonzales et al., 2012; Gonzales et al., 2014; Hatch & Gonzales, 2008; Magaña, 2012; Pease, Davis, Edwards, & Turner, 2006; Porter & Massong, 2004a, 2004b; Valdez et al., 2019) are strong evidence that spawning is most likely taking place in these sheltered, low-velocity habitats. In 2008–2009, Gonzales et al. (2014) found that of 11,602 adult RGSM in restored and natural floodplains of the MRG, 40%, 27% and 12% were gravid females, ripe males and spent females, respectively. Of 127 adults examined by Valdez et al. (2019) from six restored floodplains in 2016, 13%, 14% and 9% were gravid females, ripe males and spent females, respectively, compared to 42%, 36% and 22% for 292 adults examined from the four restored sites of this study in 2017.

The specific spawning locations of RGSM probably vary by year, depending on flow condition. In a high flow year, spawning likely takes place in floodplains and mainstem banklines where inundated vegetation provides low-velocity habitat that allows the fish to school and release and fertilize eggs in the water column, reducing the amount of downstream transport of propagules. In moderate water years, there is less flooding of vegetated banklines and less floodplain inundation that increases the chance of downstream transport of eggs and larvae. In low water years, there is virtually no floodplain or bankline inundation and a high likelihood of downstream transport of propagules. Egg buoyancy and transport are influenced by water quality, such as turbidity and salinity (Cowley et al., 2009), and at least one study indicates that the lack of quiet water refugial habitat can exacerbate the likelihood that newly spawned eggs and hatched larvae will remain continuously exposed to strong river currents, minimizing their potential survivorship (Harvey, 1987).

4.4 | Spawning dates of RGSM

Based on estimated hatch dates from an otolith-based model (Zipper et al., 2020), the earliest estimated spawning by RGSM in 2017 was 12 April in restored floodplains of the Angostura Reach. This date is similar to the earliest estimated spawn dates in 2016 for restored floodplains in the Angostura and Isleta reaches of 9 April and 7 April, respectively (Valdez et al., 2019) (Table 4). The earliest spawning from mainstem banklines of the Angostura, Isleta and San Acacia reaches in 2017 was 23 April, 17 April and 15 April, respectively. River temperatures at the Alameda Bridge at first spawning for 2016 and 2017 were 12.5°C and 12.9°C, respectively, and the ACDD was similar at 692 and 777. Based on larvae found along banklines, the estimated peaks of spawning for the Angostura, Isleta and San Acacia reaches in 2017 were 26 May, 10 May and 8 May, respectively, which helps to explain why the numbers of protolarvae were low or rapidly declining with the start of this study on 8 May. Estimated spawning in the three reaches lasted until the end of May. These findings suggest that river temperature is an important cue to timing of spawning, although increased catches of adult RGSM in restored floodplains were concurrent with sharp increases in flow, suggesting that flow was the final cue, as reported by others (Dudley et al., 2018). In all likelihood, photoperiod initially cues ova maturation in females, followed by temperature that leads to ovulation and spawning readiness, and flow increase cues the act of spawning.

Krabbenhoft et al. (2014) reported that RGSM were among the earliest spawners in the MRG, based on first appearance of young of year (~1 May from 2008 to 2010). Our 2017 study and that of Valdez et al. (2019) more accurately estimated hatch and spawn dates from growth and otolith models of larval RGSM and confirm spawning by the species starting the second week of April. Although adult RGSM were not the dominant floodplain species, their larvae were predominant in 2016 (73% in restored floodplains) and 2017 (80% in restored floodplains and 90% in mainstem banklines). This dominance was concurrent with the highest spring flows in both years and reinforces the hypothesis that the species is floodplain dependent.

4.5 | Residence time of RGSM larvae in floodplains

All cyprinid fishes undergo an initial altricial larval stage of development that requires sheltered, productive, low-velocity habitats for survival and growth. In most lowland river systems, these sheltered habitats occur as features that become inundated with spring run-off, such as low-lying riverside areas and floodplains (Pease, Davis, Edwards, & Turner, 2006; Rolls & Wilson, 2010) and tributary inflows (Lorig, Marchetti, & Kopp, 2013). Seasonal inundation of riverside areas significantly increases the total area of available aquatic habitat that offers slow, shallow, warm, productive habitat not found in the main channel at high flow. Seasonal reinundation of these low-lying areas also initiates a surge of biological productivity of algae, diatoms and invertebrates in synchrony with the energetic needs of the young fish (Junk et al., 1989; Magaña, 2012; Valdez, Beck, Medley, Schmidt-Petersen, & Zeiler, 2015; Watson, Sykes, & Bonner, 2009).

To understand residence time of larval RGSM in floodplains, we assessed the presence of all four developmental phases in restored floodplain sites and mainstem banklines (i.e., protolarvae, flexion mesolarvae, postflexion mesolarvae and metalarvae), as well as juveniles. The development of these larval phases was described in a laboratory by Platania and Dudley (2003) and in a species account by Brandenburg et al. (2018). Protolarvae are up to 6 days old and 4–5 mm long, have developing fin folds, possess a yolk sac and start feeding at 2–3 days of age. The mesolarval phase is characterized by two sub-phases. The flexion mesolarvae are 7–9 days old and 6–7 mm long and have developing caudal fin rays and a completely absorbed yolk sac, and the postflexion mesolarvae are 10–21 days old and 8–10 mm long, have developing rays on all fins and are capable of swimming. The metalarvae are 22–48 days old and 10–16 mm long, have fully developed fins and have the best swimming ability of any of the larval phases (see Valdez et al., 2019, for descriptions of larval swimming abilities).

The ongoing proportions of these developmental phases in restored floodplain sites and mainstem banklines showed the transition of these individuals from one phase to the next over a period of about 40 days during the time of persistent inundation. Few protolarvae in the floodplains in 2017 suggest that hatching had either occurred before sampling began. The greater proportion of flexion mesolarvae and decreasing proportions of postflexion mesolarvae and metalarvae in floodplains reflect not only a transition to the next phase but also a departure of individuals from floodplains to the mainstem. We recognize that changes in proportions of RGSM by larval phase may be due to other factors, such as differential predation in floodplains. The hypothesis that RGSM larvae leave the floodplains during their larval stage is supported by a much greater proportion of postflexion mesolarvae, metalarvae and especially juveniles in the mainstem, suggesting that individual larvae intentionally or inadvertently left the still-inundated floodplains starting at about 10–22 dph.

The fish at these life stages have developing or fully developed fins and fin rays and are fully capable of swimming.

5 | SUMMARY AND RECOMMENDATIONS

The sum of information from the past 17 years of floodplain investigations in the MRG provides compelling evidence that many species of the riverine fish community use and rely on floodplains for various aspects of their life history, including refuges from high mainstem spring flows, feeding, spawning, egg incubation and larval nurseries. These studies also provide strong evidence that the restored floodplain sites are similar to and function as natural floodplains.

Studies of MRG floodplains are beginning to show that the positive relationship between spring river discharge and October CPUE of RGSM is driven by egg production and larval survival through approximately 40 dph. The timing, magnitude and duration of spring run-off are important to synchronize floodplain inundation with hatching of young larvae for shelter and food. This aspect of the life history of the RGSM appears to establish the year-class strength that is reflected in the annual October census, as well as the brood stock for the following spring production period. Fish population monitoring shows that the majority of RGSM spawners are Age 1 fish (Dudley et al., 2018). We acknowledge that there may be other influencing factors such as the size of the pre-existing brood stock, the effect of augmentation from hatchery RGSM stocked in November and channel drying during summer irrigation season. But our current understanding is that the production strategy of the 2016 biological opinion (USFWS, 2016) is largely an artefact of the relationship of spring discharge to reproductive success and survival of larvae that set the year-class strength and in turn determine the CPUE density of the annual October census.

Drawbacks to promoting floodplain restoration and inundation in the MRG include a water depletion effect and creating habitat for alien species. Depletion of water occurs when water that would otherwise flow downstream for human use remains in floodplains and is lost to ground water or evapotranspiration. Newly created floodplains can become quickly vegetated by invasive riparian species, such as tamarisk, Russian olive and pampas grass. Floodplain habitats are also preferred habitat of some non-native fish species that may otherwise struggle to survive and reproduce in the mainstem, such as common carp, white sucker and channel catfish. Of the 16 fish species found in floodplains in this study, six are not native to the MRG and could expand populations with the additional floodplain habitat. Restoration of floodplain habitat and flow management are a recognized strategy for restoring ecosystem health in other desert rivers, including the Green River in Utah (Crowl et al., 2002), the Cosumnes River of central California (Moyle et al., 2007) and the Murray–Darling Basin of Australia (Rolls & Wilson, 2010). Moyle et al. (2007) reported extensive use of restored floodplains by fishes of the Cosumnes River of Central California but acknowledged that these habitats also benefited invasive predatory species, as did Crowl et al. (2002) for restored floodplains of the Green River, Utah.

Our floodplain studies provide a perspective of the mechanisms behind the relationship between spring discharge and RGSM abundance in medium (2016) and high (2017) water years. These studies are beginning to show that discharge of sufficient magnitude and duration is necessary to provide essential habitat for larval growth and survival and for eventual recruitment to the adult population. Habitat restoration in the MRG has enabled this relationship to become manifest at medium to high discharges of about 1500 ft^3/s and higher. But in years of low flow, when discharge is not sufficient to inundate much floodplain habitat, the CPUE of RGSM during the annual October census is low, presumably because there is little sheltered and low-velocity habitat for spawning, egg incubation and larval nursery. These are conditions in which the hypothesis of downstream transport of propagules is realized and when most propagules are lost from the system. These low water years become a limiting factor for the RGSM population.

Much remains to be learned about the relationships among restored floodplains, spring run-off and RGSM abundance in the MRG. For example, newly restored floodplains lack a seed and egg bank of pre-existing algae and zooplankton otherwise found in natural ephemeral floodplains (Havel, Eisenbacher, & Black, 2000), and it may take years of periodic flooding to establish these as a reliable food base for the fish (Goździejewska et al., 2016). If allochthonous material is being delivered into newly inundated floodplains as a major source of organics, the amount and type of material, as well as sedimentation rate, may be critically determined by the juxtaposition of the floodplain opening to the river channel and the thalweg (Caplan & McKenna, 2019; Crowl et al., 2002).

Observations, measurements and analyses from this and other studies reveal important aspects of the variables associated with floodplain habitats beneficial to the MRG fishes, especially the endangered RGSM. The following summarizes those aspects as recommendations for future construction or modification of restored floodplains along the MRG:

- *Size, location and elevation*. About 300 floodplain sites, 0.4 to 5 ha in size, have been constructed in the MRG since in 2003. Adults, eggs and larvae of RGSM have been found in all sites sampled, and there is no evidence that site size contributed to fish use. The size of restored floodplain sites should be determined by the available space and riverside condition, and small areas as well as large can function as suitable habitat. Floodplain location is more critical than size, as floodplains with open access in the path of river currents have the greatest numbers of eggs and larvae (Porter & Massong, 2004a), but additional work is needed to better determine the effect of river currents on entrainment and as fish attractants. The numbers of RGSM in a given floodplain may also be related to proximity of population concentrations and to inter-annual variation in fish abundance. Floodplain elevation is also critical as restored sites have been constructed to inundate starting at about 1500 ft^3/s (Fluder, Porter, & McAlpine, 2007; Tetra Tech, Inc., 2004), which is exceeded by mean monthly discharge (1973–2017) of 1810, 2790 and 2390 ft^3/s for April, May and June, respectively, for the Rio Grande at Albuquerque (USGS 08330000). However, in some years, peak spring run-off does not reach 1500 ft^3/s, and production and recruitment of RGSM is low, suggesting that floodplains that inundate at 1000 ft^3/s and lower are necessary. Recent studies of newly restored floodplains are investigating inundation at flows of about 800 ft^3/s (McKenna et al., 2020). Different floodplains that inundate at different flows also provide a greater diversity and opportunity for RGSM to find suitable habitat.

- *Contour and depth*. This study showed that RGSM larvae in floodplains were at greater and more varied distances from the water's edge than larvae along mainstem banklines. Two factors appear to drive these locations, one is that the restored sites are flat, generally vegetated throughout with terrestrial plants and relatively shallow when inundated, allowing the larvae to distribute more broadly. The second factor is that proximity to high velocity and deep water in the mainstem confine the larvae to near shore where vegetation buffers velocity and provides cover. Floodplains should be contoured to inundate at various flows so that low-velocity, shallow habitat is available through a range of flows. Mainstem banklines should be contoured with irregularities to widen the band of available habitat.
- *Cover and canopy*. Cover is an important feature to RGSM larvae, but mechanical revegetation may not be necessary, as it appears that the natural terrestrial vegetation in restored floodplains provides sufficient cover for fish to hide and feed. In-water cover appears to be important in both floodplains and banklines. Most of the cover is in the form of vegetation, primarily terrestrial plants that are present in the area year round and become seasonally inundated with spring run-off. Overhead canopy varies at floodplain sites and along mainstem banklines, but there does not appear to be a strong correlation with presence of RGSM larvae. The floodplains and banklines of the MRG that inundated in spring had extensive ground cover of herbaceous plants and stands of terrestrial woody vegetation that included cottonwood, Russian olive, willow and tamarisk, as well as debris piles which were all used by the larvae.
- *Temperature*. RGSM larvae were found in the warmest water available in both restored floodplains and mainstem banklines, although temperature is not a variable that can be managed in the MRG. It appears that ACDDs of about 700–900 are an important cue for spawning, along with flow increases and spikes. Possibly, ACDDs can be used to predict spawning time of RGSM and to manage timely flow releases that will inundate floodplains used for spawning and larval nurseries.
- *Timing and duration*. The timing of floodplain inundation is critical to ensure that maximum nursery habitat is available for the newly hatched RGSM larvae. This increases the likelihood for a suitable food supply, as newly reinundated floodplains typically surge with production of diatoms, algae and small invertebrates in synchrony with the dietary needs of the young fish. Ideally, floodplain inundation should begin about the time of spawning, as indicated by ACDDs of about 700–900, persist for about 30–40 days during the entire hatch cycle and allow individual larvae to fully develop fins and fin rays (14–22 dph, Valdez et al., 2019).

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CONFLICT OF INTEREST

The authors declare no conflicts of interest in the development of this manuscript.

DATA AVAILABILITY STATEMENT

The data used in this analysis are available from the NMISC.

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