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RESEARCH ARTICLE

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Managed spring runoff to improve nursery floodplain habitat for endangered Rio Grande silvery minnow

Richard A. Valdez[1] | **Grace M. Haggerty**[2] | **Kenneth Richard**[2,3] | **Deanna Klobucar**[1,4]

[1] SWCA Environmental Consultants, Logan, UT, USA
[2] New Mexico Interstate Stream Commission, Albuquerque, NM, USA
[3] U.S. Bureau of Reclamation, Albuquerque, NM, USA
[4] Institute of Arctic Biology, University of Alaska, Fairbanks, AK, USA

Correspondence
Richard A. Valdez, SWCA Environmental Consultants, 172 West 1275 South, Logan, UT 84321, USA.
Email: rvaldez@swca.com

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Abstract

Water managers in New Mexico, USA, stored water in El Vado Reservoir and coordinated releases into the Chama River that augmented the runoff of the Rio Grande, resulting in a discharge >1,500 ft^3/s (42.5 m^3/s) for 35 days (May 17 to June 20, 2016) at Albuquerque. The managed runoff inundated over 400 ha of previously restored floodplains in the Middle Rio Grande, thereby providing spawning and nursery habitat for the endangered Rio Grande silvery minnow (*Hybognathus amarus*, RGSM). Spawning began April 9 at annual cumulative degree-days of 717, during daily increases in discharge of 200–300 ft^3/s (5.7–8.5 m^3/s), and hatch dates were normally distributed over 53 days (April 11 to June 3). RGSM were 73% of larvae collected in six restored floodplain sites and found in shallow water (mean = 19.6 cm), low velocity (mean = 3.9 cm/s), near vegetative cover, and with 75% within 1 m of the water's edge. Declining proportions of early to late larval phases and a near absence of juveniles indicate a gradual departure from floodplains as postflexion mesolarvae and metalarvae 14–22 days post hatch (dph), with most leaving by the juvenile stage 40 dph. The annual RGSM October census showed an increase of 0.16 to 7.20 fish/100 m^2 from 2015 to 2016, indicating that the managed runoff resulted in a positive population response. This study showed that constructing floodplains and managing river and reservoir operations to inundate those floodplains during and after RGSM spawning can provide nursery habitat that improves reproductive success and recruitment.

KEYWORDS

degree-days to spawning, larval hatch time, managed runoff, nursery habitat, restored floodplains, Rio Grande silvery minnow

1 | INTRODUCTION

Floodplain formation during spring runoff is an important feature of arid-land rivers that provides sheltered productive habitats for fish feeding, spawning, and nurseries (Galat et al., 1998; Graham & Harris, 2005). Many rivers in western North America have been modified by flood control, water use, and ongoing climate change, causing riverside floodplains to become delinked from the main channel and negatively affecting riparian habitats and associated species (Petts, 2009). Managed releases from dams and reservoirs have been implemented to simulate a natural hydrograph and restore floodplain connection to benefit fish species (Chen & Olden, 2017), but reduced river volume and channel degradation have necessitated mechanically lowering floodplain inundation levels and coordinated water releases (Holden, 1999; Patno, LaGory, Chart, & Bestgen, 2012; Valdez & Nelson, 2004).

The Rio Grande is a medium-size river of the southwestern United States, in which the abundance and diversity of native fishes have declined over the last few decades as flood control and river regulation have reduced the frequency and magnitude of overbank flooding (Molles, Crawford, Ellis, Valett, & Dahm, 1998). Two native broadcast spawning species that relied on nursery floodplains are now extirpated from the Rio Grande (i.e., phantom shiner, *Notropis orca*; and Rio Grande bluntnose shiner, *Notropis simus simus*), and a third, the Rio Grande silvery minnow (*Hybognathus amarus*, RGSM), was listed as federally endangered in 1994 (U.S. Fish and Wildlife Service (USFWS), 1994). The RGSM has declined to about 5% of its original range, and the only remaining wild population is found in the Middle Rio Grande (MRG), New Mexico (Bestgen & Platania, 1991).

The MRG is a 280-km reach of river between Cochiti Dam and Elephant Butte Reservoir (Figure 1). This river reach was historically a wide, shallow, braided channel that migrated laterally with expansive and variable spring flooding, but the contemporary river has been diked and narrowed for flood control and regulated by water operations (Massong, Tashjian, & Makar, 2006). These geomorphic changes and flow regulation have decoupled much of the historic floodplain from the active river channel (Magaña, 2012) and disrupted the synchrony of floodplain inundation with the reproductive phenology of spring broadcast spawning fishes (Krabbenhoft, Platania, & Turner, 2014; Turner, Krabbenhoft, & Burdett, 2010).

The Middle Rio Grande Endangered Species Collaborative Program (MRGESCP; http://www.ose.state.nm.us/Basins/RioGrande/) was established in April 2002 under a Memorandum of Understanding to address issues arising from Endangered Species Act listings in the MRG. In recognition of the need for floodplains and riparian areas, the USFWS issued a 2003 biological opinion (USFWS, 2003) that directed federal agencies to "… conduct habitat/ecosystem restoration projects in the Middle Rio Grande to increase backwaters and oxbows, widen the river channel, and/or lower river banks to produce shallow water habitats, over-bank flooding, and regeneration of stands of willows and cottonwood to benefit the Rio Grande silvery minnow." Since 2003, the MRGESCP has created or restored about 1,600 ha of habitat under a water depletion-neutral framework that mechanically modifies banklines, islands, and old floodplains to create backwaters, embayments, terraces, and depressions that inundate at discharges of 500 ft^3/s (14.2 m^3/s) to 3,500 ft^3/s (99.1 m^3/s; Tetra Tech, Inc., 2004). The 2016 biological opinion (USFWS, 2016) further identified (a) large-scale habitat restoration and (b) conservation storage of water for release to inundate those habitats, as two of four key conservation needs for a RGSM recovery and survival strategy.

Nearly 300 sites ranging 0.4–5 ha in size have been constructed in the MRG as features designed to seasonally inundate and entrain eggs and larvae of RGSM in spring and to restore native riparian vegetation and floodplain dynamics (SWCA, 2016). Recent investigations show that these restored sites entrain and retain RGSM eggs as effectively as natural floodplains (Porter & Massong, 2004) and that gravid and ripe adults are abundant in both, indicating that the species spawns in these habitats (Gonzales, Tave, & Haggerty, 2014). These floodplains and other low-velocity areas of the MRG are also important nursery habitat for larval RGSM (Magaña, 2012), where they are often more abundant than other species (Pease, Davis, Edwards, & Turner, 2006).

The RGSM is a small, spring-spawning, riverine cyprinid that matures in its first year of life and may live up to 5 years in the wild (Cowley, Shirey, & Hatch, 2006). Adults school and release and fertilize semibuoyant eggs in the water column that hatch in 2–4 days as altricial larvae. It is hypothesized that mainstem spawning results in long-distance transport of pelagic eggs and larvae with a subsequent upstream return of fish to natal areas (Dudley & Platania, 2007; Platania & Altenbach, 1998). Alternatively, the RGSM is thought to be primarily a demersal floodplain spawning species with evolved eggs that are secondarily buoyant in high sediment environments created by expansive flooding, with little downstream transport of propagules (Medley & Shirey, 2013). A series of laboratory and floodplain studies have been conducted to inform these hypotheses (e.g., Gonzales et al., 2014; Hutson, Toya, & Tave, 2018; Tave, Toya, & Hutson, 2018; Widmer, Fluder, Kehmeier, Medley, & Valdez, 2012), including the current study.

A positive correlation between high spring discharge and RGSM October catch per unit effort (CPUE; Dudley, Platania, & White, 2016a; USFWS, 2016) suggests that the species is floodplain dependent, but the mechanisms for this relationship are poorly understood. This paper explores this relationship during a managed spring runoff by examining the occurrence of RGSM in floodplains, including their temporal abundance as adults; time of spawning relative to timing, duration, and magnitude of runoff; residence time of larvae; and habitat features used by the larvae.

2 | METHODS

2.1 | Coordinated water storage and release

In spring 2016, water managers in New Mexico coordinated water releases from tributary reservoir storage to augment the natural runoff of the mainstem Rio Grande. The storage and release of 31,593 acre-feet (38,969,966 m^3) of water from El Vado Reservoir on the Chama River required the approval of the Rio Grande Compact Commission[1] to modify dam operations for the purpose of temporarily storing water and timed releases. The releases on May 20 to June 14 were intended to augment the natural flow of the mainstem Rio Grande and to aid in creating a spawning flow for the benefit of the RGSM (U.S. Bureau of Reclamation, 2017). A concurrent spike release was made for channel maintenance of the Chama River. These releases increased the magnitude and duration of spring runoff and inundated restored floodplains of the MRG, 200–480 km downstream of El Vado Dam.

The May–June discharge was coordinated through a series of dam releases and water transfers by the New Mexico Interstate Stream Commission, Middle Rio Grande Conservancy District, Albuquerque Bernalillo County Water Utility Authority, U.S. Bureau of Reclamation, and U.S. Army Corps of Engineers. The timing and magnitude of releases

[1]Storage of water at El Vado Reservoir began May 6, 2016, for release to the Middle Rio Grande Valley under the "31 March 2016 Rio Grande Compact Commission (RGCC) Resolution Regarding Temporary Modification of Operations at El Vado Reservoir in New Mexico During May and June 2016."

from El Vado Dam on the tributary Chama River were planned to coincide with maximum discharge of the mainstem Rio Grande and with operations at Abiquiu and Cochiti reservoirs in north central New Mexico (Figure 1). The shape of the hydrograph was not planned in advance, but the intent of the managed runoff was to create the maximum stage and duration possible for the available water volume.

2.2 | Study sites

Sampling was conducted May 20 to June 17, 2016, in six restored floodplain sites of the MRG, that is, four in the Angostura reach and two in the Isleta reach (Figure 1). The six sites were constructed during 2007–2015 to inundate above 1,500 ft^3/s and included Willow Creek (5.30 ha), Albuquerque Bernalillo County Water Utility Authority (ABCWUA) SE (1.87 ha), ABCWUA SW (3.01 ha), Tingley (2.57 ha), Willie Chavez North (2.77 ha), and Willie Chavez South (2.23 ha). Each site was sampled six to eight times with a 3-day interval between samples. The number of samples collected by site and gear type are presented in Table 1, and photographs of sites are provided in Figure 2.

2.3 | Fish and egg sampling

Large fish were sampled with D-frame double wing fyke nets (2.1 m long × 1.0 m wide × 0.60 m high; wings 0.6 m high × 4.6 m long; 3.1-mm Delta Mesh; 5-cm-diameter throat). Nets were placed for 3–

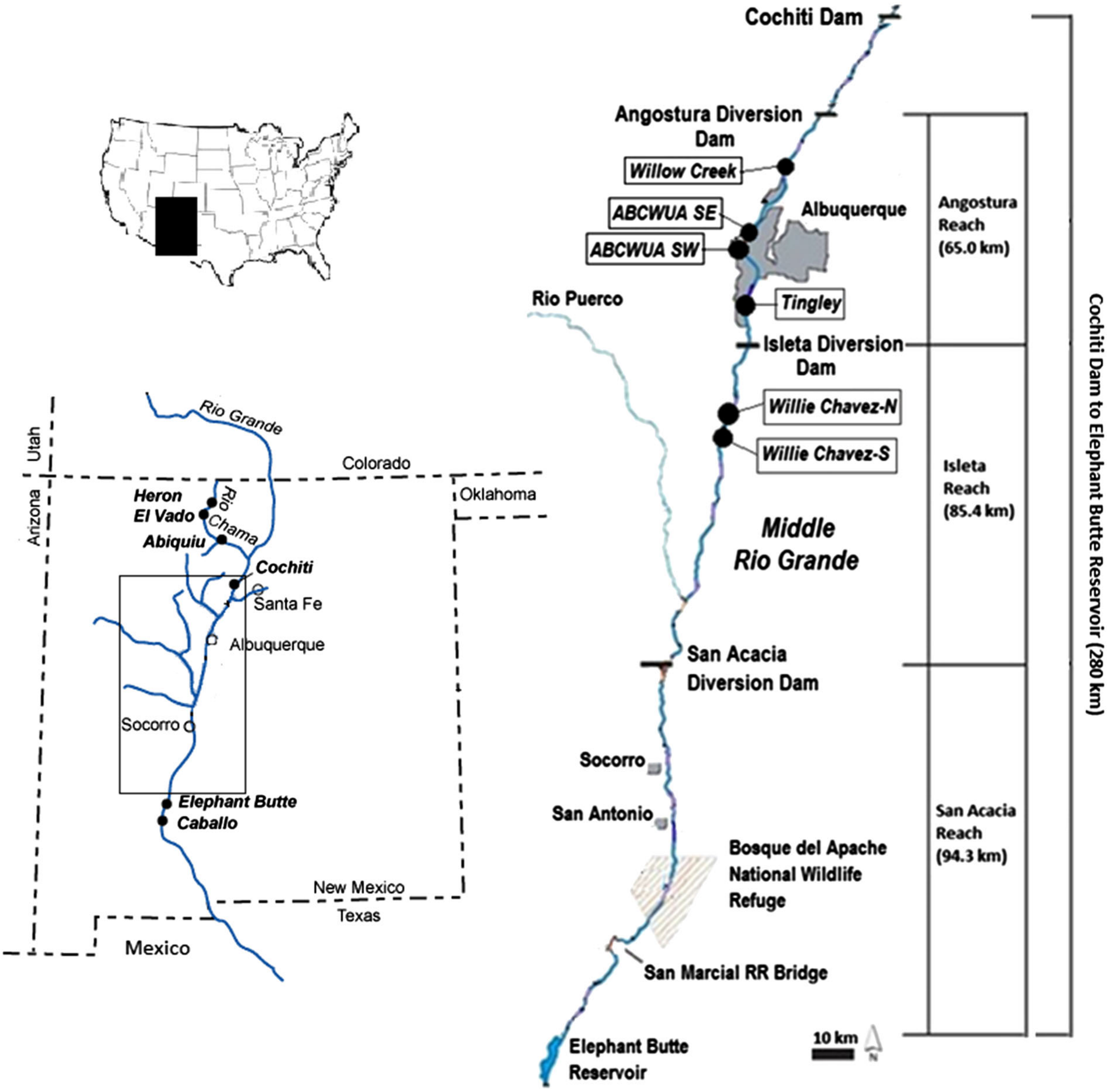

FIGURE 1 Major dams (filled circles) of the Rio Grande in New Mexico (left inset) and the Middle Rio Grande (right inset) showing the six floodplain restoration sites sampled (filled circles) and the three reaches between dams. ABCWUA, Albuquerque Bernalillo County Water Utility Authority

TABLE 1 Number of samples taken by gear type in six restoration sites in the Angostura and Isleta reaches, May 20 to June 17, 2016

	Albuquerque reach				Isleta reach		
Gear type	ABCWUA SE	ABCWUA SW	Tingley	Willow Creek	Willie Chaves South	Willie Chaves North	Total
Fyke nets	32	30	44	39	21	20	186
Dip nets	197	231	218	213	192	195	1,246
Drift nets	39	62	41	67	42	39	290
MECs	39	49	44	50	30	30	242
Light traps	1	2	1	0	1	0	5
Total	308	374	348	369	286	284	1,969

Abbreviations: ABCWUA, Albuquerque Bernalillo County Water Utility Authority; MECs, Moore egg collectors.

6 hr at the inflow, outflow, and approximate midpoint of each site. All fish collected were identified and released near the capture location. Standard length (SL) in millimetres and reproductive condition were recorded for RGSM, and each was examined for PIT (Passive Integrated Transponder) tags or elastomer tags from other studies.

Four gear types were used to collect eggs and larvae, including dip nets, drift nets, Moore egg collectors (MECs; Altenbach, Dudley, & Platania, 2000), and light traps. Long-handled D-frame dip nets (30 cm × 20 cm with 243 μm Nitex mesh) were used to take standardized 1-m sweeps at random locations in each of four cover types: open water, terrestrial woody, terrestrial herbaceous, and aquatic vegetation. Maximum area of inundated habitat for each cover type was measured at each site with a Trimble GeoXT handheld GPS and processed with ArcGIS. Depth, velocity, distance to water's edge, and cover type were recorded for each dip-net sweep as a sample location. Dip nets have not been used previously in the MRG and were used to sample eggs and larvae because they were less likely to disturb the floodplain and fish community than other active gears, such as seines or electrofishing; federal and state permitting agencies requested that sampling be conducted with minimum disturbance to nursery habitat. Dip nets also provided specific capture locations for correlating individual fish occurrence with habitat variables.

Fine-mesh drift nets and MECs were placed in tandem at water depths of 30–76 cm at the inflow and outflow of each site to estimate the density of eggs and larvae being transported by flow into and from each site. Drift nets had a 30-cm-high and 46-cm-wide rectangular opening and were 1.5 m long with 0.75-mm mesh. The MECs were set for 2 hr and the drift nets for 10 min with the top of the gear even with the water's surface, and each was held in place with metal posts driven into the substrate. Water velocity was measured at the mouth of each drift net and MEC at the beginning and end of each set, and the count of eggs or larvae captured was expressed as number per 1,000 m^3 of water filtered. Drift nets have not been used previously in the MRG to collect eggs or larvae, and MECs are used for the annual egg survey of the MRG (Dudley, Platania, & White, 2016b).

Three quatrefoil larval fish light traps were set overnight (dusk to dawn) in select restoration sites to augment the capture of larval fish. Each trap was made of clear polycarbonate, 30 cm diameter × 25 cm high, with four 5-mm-wide entry slots, and a collection basin with a 250-μm sieve. A 12-hr glow stick was placed in each trap as a light source to attract the larvae. Light traps were previously used to sample larvae in the MRG by Pease et al. (2006), Magaña (2012), and Krabbenhoft et al. (2014).

2.4 | Processing and identification of samples

The eggs of RGSM are distinctly globular and were visually identified, enumerated, and released on site, along with unidentified eggs of other species. All larval fish were placed in labelled plastic vials with 10% formalin and transferred to a laboratory for identification by William Howard Brandenburg (DBA Lateral Lines, Albuquerque, NM). In the lab, each larva was identified to genus and species, and each RGSM was measured to the nearest 0.1 mm, with the ontogenetic developmental phase described as protolarvae, flexion mesolarvae, postflexion mesolarvae, or metalarvae (Brandenburg, 2018).

2.5 | Estimated date of spawning and hatching

The date of hatching for each larval RGSM was estimated with a temperature–growth model. The equation for 20 °C ($y = 0.14x + 3.66$, $r^2 = 0.94$; Platania & Dudley, 2003) was inverted ($x = [y - 3.66]/0.14$) to compute the estimated number of days post hatch (dph, x) from the SL of each larva (y). The laboratory-based growth equation was developed for up to 50 dph, and fish estimated to be older were removed from further analysis to avoid model extrapolation. The number of dph for each fish was subtracted from the collection date to determine the date of hatching, and the estimated spawning date was derived as 2 days earlier (Platania & Altenbach, 1998). The earliest hatch date was the day followed by consistent daily occurrences of estimated hatching, and earlier outliers were discounted. A more resolute age determination of RGSM larvae is being done with otolith daily growth rings in a related study (S. Zipper, SWCA, personal communication, June 25, 2019). Other methods have been used to estimate hatching dates of fish, including the date of first appearance of larvae as a proxy for the onset of spawning (Krabbenhoft et al., 2014); an inverse prediction procedure and regression to known size at hatch, by using larval lengths from periodic samples (Falke, Fausch, Bestgen, & Bailey, 2010); and a temperature threshold (Fraser, Bestgen, Winkelman, & Thompson, 2019).

FIGURE 2 Dip nets at (top) ABCWUA SW and (middle left) Tingley; (bottom left) fyke net in Willie Chavez; and (right) aerial of ABCWUA SE. Photos by Pauletta Dodge, Ken Richard, Todd Caplan, and Ondrea Hummel, respectively. ABCWUA, Albuquerque Bernalillo County Water Utility Authority

We also calculated annual cumulative degree-days (ACDDs) as the accumulated sum of mean daily water temperature at the Alameda Bridge, starting January 1 to the earliest estimated spawning date. Degree-days, as the accumulated temperature experienced by a fish, is used as an indicator of growth, maturation, and spawning readiness (Chezik, Lester, & Venturelli, 2014).

3 | RESULTS

3.1 | Managed runoff

The discharge of the managed runoff for the Rio Grande at Albuquerque (U.S. Geological Survey [USGS] #08330000) remained above 1,500 ft^3/s (42.5 m^3/s) for 35 days (May 17 to June 20) and above 2,500 ft^3/s (70.8 m^3/s) for 23 days (May 25 to June 16), with a peak of 3,510 ft^3/s (99.4 m^3/s) on June 7 (Figure 3). Without the managed releases, the predicted peak discharge at Albuquerque would have been only about 2,900 ft^3/s (82.1 m^3/s), with a sustained discharge above 1,500 ft^3/s for 28 days and above 2,500 ft^3/s for only 5 days. The managed runoff remained above 2,500 ft^3/s for 18 days longer than would have otherwise occurred and inundated about 400 ha of restored floodplains above 1,500 ft^3/s for 7 days longer.

3.2 | Fish species composition

Altogether, 717 fishes representing 10 species were captured with fyke nets in the six restoration sites (Table 2). The red shiner (*Cyprinella lutrensis*) was the most common species, comprising 75% of total catch, and the RGSM was the second most common with 18%. The eight other species each comprised less than 3% of total catch. The highest CPUE and counts of RGSM were at the ABCWUA SW site (1.21, 35) and the Tingley site (0.69, 50); no RGSM adults were caught at the Willie Chavez North site (Figure 4).

Adult RGSM (n = 127) in fyke nets ranged in size 50 to 89mm SL (mean = 63 mm), and included 18 (14%) males expressing milt, 16 (13%) gravid females, and 12 (9%) spent females. The remaining 81 (64%) were of undetermined gender and reproductive condition. Four of the RGSM were marked hatchery fish (released by the USFWS as part of an augmentation program), and the remaining 123 were unmarked fish of wild origin.

Altogether, 2,562 larval fish of nine species were collected with four gear types from the six restoration sites (Table 3). The RGSM, common carp (*Cyprinus carpio*), and fathead minnow (*Pimephales promelas*) were

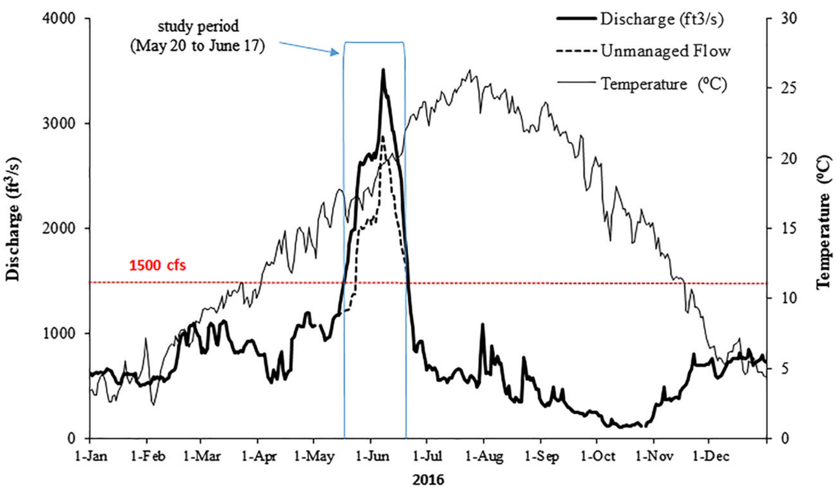

FIGURE 3 Mean daily discharge of the Rio Grande at Albuquerque (U.S. Geological Survey #08330000) under the managed flow and predicted for the unmanaged flow and mean daily temperature of the Rio Grande at the Alameda Bridge (U.S. Geological Survey #08329918). The managed spring flow released 31,593 acre-feet (38,969,966 m^3) of water from El Vado Reservoir May 20 to June 14, 2016, and the study was conducted May 20 to June 17. Horizontal dashed line shows discharge of 1,500 ft^3/s where inundation of the six study sites began

TABLE 2 Number of fishes captured with fyke nets and total percent composition for the six restoration sites in the Angostura and Isleta reaches, May 20 to June 17, 2016

	Angostura reach				Isleta reach			
Species	Willow Creek	ABCWUA SE	ABCWUA SW	Tingley	Willie Chaves-N	Willie Chaves-S	Total	Percent
Red shiner, *Cyprinella lutrensis*	72	197	3	206	8	49	535	74.62
Rio Grande silvery minnow, *Hybognathus amarus*	17	19	35	50	0	6	127	17.71
Flathead chub, *Platygobio gracilis*	6	2	0	9	0	0	17	2.37
Fathead minnow, *Pimephales promelas*	3	8	1	2	0	1	15	2.09
Common carp, *Cyprinus carpio*	0	0	4	0	3	0	7	0.98
Channel catfish, *Ictalurus punctatus*	0	0	2	2	2	0	6	0.84
White sucker, *Catostomus commersonii*	1	0	4	0	0	0	5	0.70
White crappie, *Pomoxis annularis*	0	0	0	1	1	1	3	0.42
Yellow bullhead, *Ameiurus natalis*	0	0	1	0	0	0	1	0.14
Western mosquitofish, *Gambusia affinis*	0	0	0	1	0	0	1	0.14
Total fish captured	99	226	50	271	14	57	717	100

Abbreviations: ABCWUA, Albuquerque Bernalillo County Water Utility Authority.

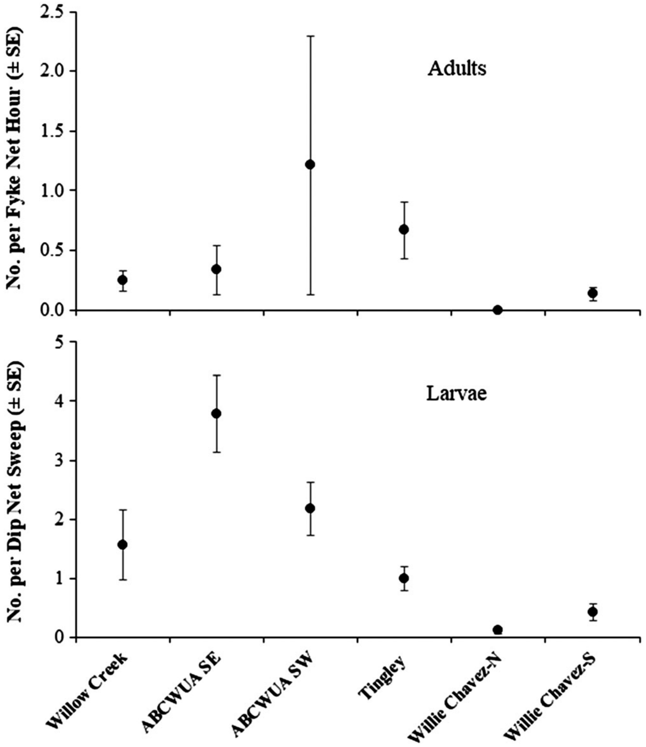

FIGURE 4 Catch per unit effort of Rio Grande silvery minnow adults with fyke nets and larvae with dip nets by restoration site. Sites are ordered left to right as upstream to downstream. ABCWUA, Albuquerque Bernalillo County Water Utility Authority

TABLE 3 Number of larval fishes by species and gear type for the six restoration sites

Species	Dip net	Drift net	Light trap	MEC	Total	Percent
Rio Grande silvery minnow	1,638	76	119	39	1,872	73.07
Common carp	158	31	42	34	265	10.34
Fathead minnow	172	11	1	2	186	7.26
White sucker	70	6	12	7	95	3.71
Red shiner	8	0	48	0	56	2.19
Unidentified Cyprinidae	47	0	0	0	47	1.83
Western mosquitofish	33	0	0	0	33	1.29
River carpsucker	6	0	0	0	6	0.23
Bluegill	1	0	0	0	1	0.04
Yellow perch	0	0	1	0	1	0.04
Total	2,133	124	223	82	2,562	100

Note. River carpsucker (*Carpiodes carpio*), bluegill (*Lepomis macrochirus*), and yellow perch (*Perca flavescens*) were not captured with fyke nets (see Table 1).

Abbreviation: MEC, Moore egg collector.

the most abundant with 73%, 10%, and 7% of total catch, respectively (Table 4). Over 83% of all larvae were captured with dip nets (2,133), and only 17% (429) with drift nets (124), MECs (82), and light traps (223). Of 1,872 larval RGSM, 1,638 (88%) were captured with dip nets and the remaining 234 (12%) with the three other gear types.

The highest counts of larvae for most species, including the RGSM, were at the ABCWUA SE (636) and ABCWUA SW (415) sites. Of 1,638 RGSM larvae collected with 1,246 dip net sweeps, mean overall CPUE was 1.3 fish/sweep. CPUE was highest with 3.8 fish/sweep at the ABCWUA SE site and decreased downstream to 0.1 fish/sweep at the Willie Chavez North site (Figure 4), where only 20 RGSM larvae were collected and no adults were caught in fyke nets.

3.3 | Estimated time of spawning and hatching

We estimated hatching dates for 1,838 RGSM larvae by using the SL of each fish in a temperature–growth model for 20 °C. Estimated hatch dates were approximately normally distributed over a 53-day period, with respective earliest, peak, and latest hatching dates of April 11, May 11, and June 3 for 1,725 larvae in the Angostura reach; and April 9, May 5, and June 1 for 113 larvae in the Isleta reach (Figure 5). For the Angostura and Isleta reaches, the earliest estimated spawning dates (2 days prior to hatching) were April 9 and 7 at 717 and 692 ACDDs, respectively. Corresponding mean daily temperature of the MRG at the Alameda Bridge (USGS #08329918) for both dates was 12.5 °C.

The growth model for 20 °C was used because it best approximated the water temperature experienced by RGSM in the first 50 dph. Based on a peak hatch date of May 11, the mean daily river temperature at the Alameda Bridge for 50 days hence was 19.27 °C, or approximately 20 °C. We did not see a significant difference in mean daily mainstem temperature at the Alameda Bridge (18.41 °C) and the six restored floodplain sites (18.46 °C) for the study period May 20 to June 17, and the former was used to describe ambient temperature during spawning, hatching, and larval growth.

Counts of RGSM eggs collected at six MRG sites in a separate 2016 egg survey (Dudley et al., 2016b) were included in Figure 5 to illustrate the correspondence of river-wide egg collection from another study with the estimated hatching dates derived from this study. Eggs of RGSM were first collected April 23 at the downstream-most San Marcial site and May 6 at the Isleta site, a date that more closely corresponded with the estimated peak hatching date of May 5 for the Isleta reach. Highest egg count was 172 at San Marcial on April 26. The temporal distribution of eggs corresponded with the bulk of hatching times, but not with the earliest and latest hatch dates, and the egg count did not follow a particular pattern in magnitude to indicate a spawning peak, as reflected by the estimated hatch times. The annual egg survey informs the collection of eggs for hatchery propagation and augmentation but did not provide the resolution of spawning time in 2016 otherwise seen with estimated spawning and hatching dates derived from backcalculated ages of individual larvae.

3.4 | Movement and drift to and from floodplains

Forty-nine, 39, and 39 adult RGSM were caught in fyke net sets at the inflow, outflow, and midpoint of the six restoration sites, respectively

TABLE 4 Number of larval fishes by species and the six restoration sites, as collected with dip nets, drift nets, light traps, and MECs

Species Code	Willow Creek	ABCWUA SE	ABCWUA SW	Tingley	Willie Chavez-N	Willie Chavez-S	Total	Percent
Rio Grande silvery minnow	293	676	592	212	20	79	1,872	73.07
Common carp	31	40	101	16	8	69	265	10.34
Fathead minnow	29	51	79	13	12	2	186	7.26
White sucker	46	3	29	16	0	1	95	3.71
Red shiner	0	0	2	1	3	50	56	2.19
Unidentified Cyprinidae	7	17	13	10	0	0	47	1.83
Western mosquitofish	0	0	0	0	27	6	33	1.29
River carpsucker	1	2	0	0	1	2	6	0.23
Bluegill	0	0	1	0	0	0	1	0.04
Yellow perch	0	0	1	0	0	0	1	0.04
Total	407	789	818	268	71	209	2,562	100

Note. Sites are ordered left to right as upstream to downstream.

Abbreviation: ABCWUA, Albuquerque Bernalillo County Water Utility Authority; MEC, Moore egg collectors.

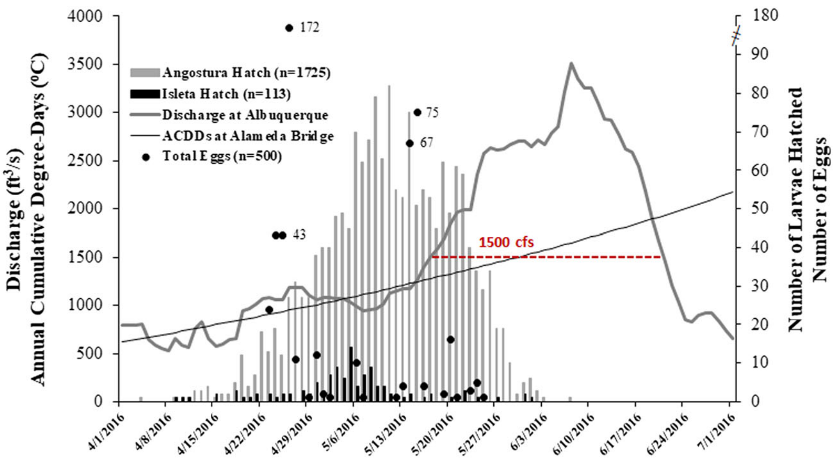

FIGURE 5 Estimated hatch dates of Rio Grande silvery minnow, based on a 20 °C temperature–growth model and standard length of larvae collected from the Angostura and Isleta reaches. Discharge is for the Rio Grande at Albuquerque (U.S. Geological Survey #08330000) and annual cumulative degree-days (ACDDs) is at the Alameda Bridge (U.S. Geological Survey #08329918). Total counts of silvery minnow eggs collected at six sites in the Isleta and San Acacia reaches from the annual egg survey (Dudley et al., 2016b) are also shown (highest counts are indicated). Horizontal dashed line shows discharge of 1,500 ft^3/s where inundation of the six floodplain sites began

(Figure 6). Adults persisted in the floodplains throughout inundation, though counts were small from an apparent year of low population abundance. No distinct pattern of movement was detected for adult RGSM with the inflow and outflow fyke net sets.

Altogether, 97 eggs and 206 larvae of RGSM were captured in drift nets and MECs at the inflow and outflow of the six restoration sites May 20 to June 17. No distinct pattern in drift was detected as eggs were found in inflow and outflow sets intermittently starting May 20 with an apparent decline and ending May 30 (Figure 6). Eggs were also captured in small numbers with dip nets within sites May 30–31 and June 7–8, but no eggs were found afterward. Drift nets and MECs filter a small volume of water near the surface, and the majority of eggs likely pass beneath the nets; fertilized water-hardened RGSM eggs are slightly denser than water (specific gravity = 1.003–1.005; Cowley, Alleman, Sallenave, McShane, & Shirey, 2009) and are moved by saltation along the bottom rather than floating near the surface. Few larvae were captured with drift nets and MECs, probably because most larval drift occurs in reduced light during crepuscular periods (Valdez, Carter, & Ryel, 1985) or possibly because the larvae stayed close to the water's edge.

Larvae of RGSM were captured in greater numbers than eggs with drift nets and MECs. One-hundred forty larvae were captured in inflow sets, and 66 in outflow sets May 27 to June 17, but with no apparent pattern in drift density into or from the sites (Figure 6). The count of larvae collected daily with dip nets at the six sites was greater (n = 1,638) and showed an increase from June 1 to 8, followed by relatively stable daily counts to the end of sampling on June 17. These data show that eggs were present in the floodplains early in the study and that larvae persisted throughout the period of inundation.

3.5 | Proportions of larval phases in floodplains

Temporal proportions of developmental larval phases were used as an indicator of larval residence time in floodplains. All four developmental phases of RGSM larvae were collected at the six sites (Figure 7). Of 1,872 larvae, the earliest phase (protolarvae) comprised 5% of total catch, flexion mesolarvae 35%, postflexion mesolarvae 41%, metalarvae 19%, and juveniles 0.1%. The daily proportion of protolarvae dropped dramatically from June 1 to 3, with a second pulse June 4–9 that corresponded with an increase in eggs and larvae onto the floodplains

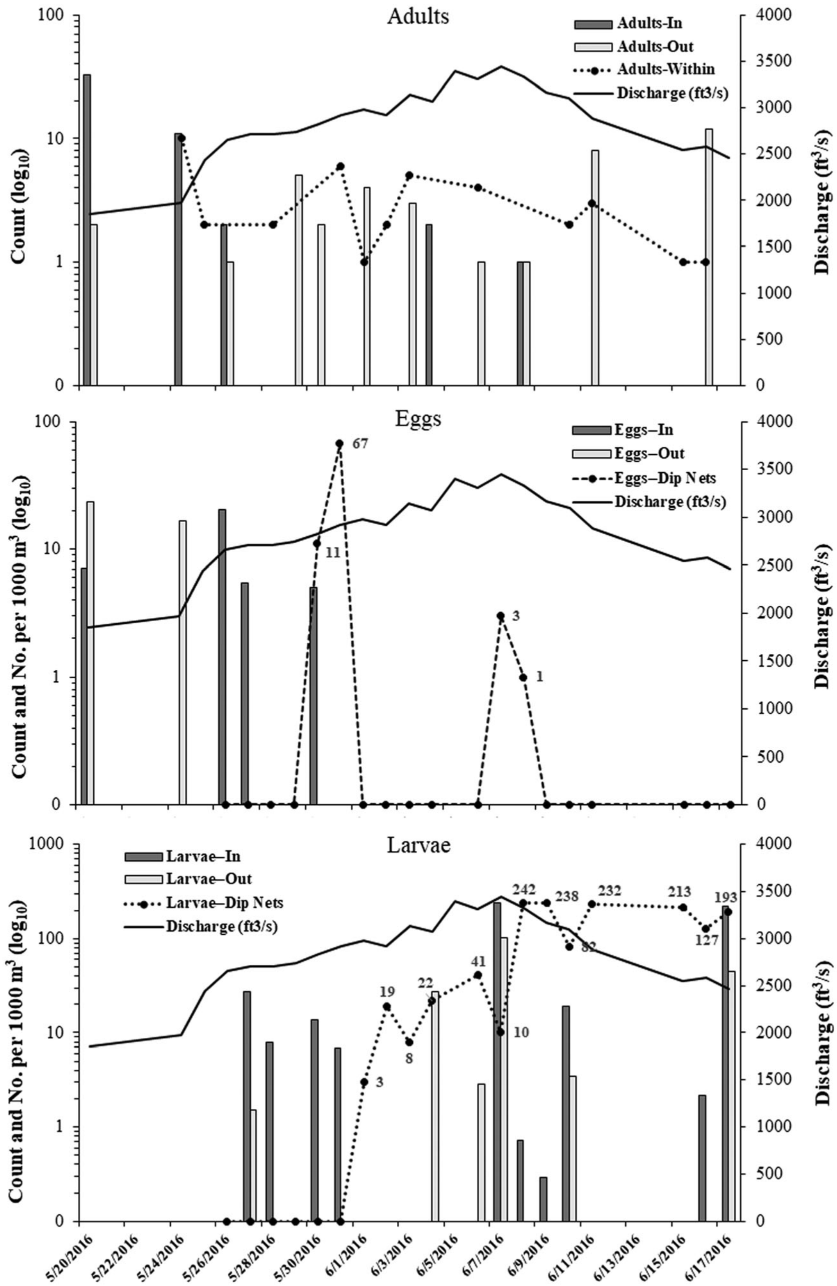

FIGURE 6 Counts of adult Rio Grande silvery minnow in fyke nets at inflow, outflow, and within the six restoration sites and mean daily drift density of silvery minnow eggs and larvae at the inflow and outflow of the sites with counts of eggs and larvae captured with dip nets within sites. Mean daily discharge of the Rio Grande at Albuquerque (U.S. Geological Survey gage #08330000) is shown on all graphs

(see Figure 6). The proportions of flexion and postflexion mesolarvae also declined over the study period, whereas the metalarvae were a smaller proportion throughout. The end of sampling on June 17 approximately corresponded with the end of inundation, at which time only postflexion mesolarvae and metalarvae were collected. Only two juvenile RGSM were collected during the entire study. Mean and range of SL for the four larval phases were as follows: protolarvae (5.4 mm, 4.4–6.3 mm), flexion mesolarvae (6.9 mm, 5.4–8.4 mm), postflexion mesolarvae (8.4 mm, 6.6–10.6 mm), and metalarvae (10.5 mm, 7.8–14.4 mm).

3.6 | Floodplain features used by larvae

Depth, velocity, distance to water's edge, and cover type were recorded for 770 dip net locations that yielded 2,084 larvae, of which 1,628 were RGSM. The RGSM larvae were found in mean water depth of 19.6 cm (range, 3.0–61.0) and mean velocity of 3.9 cm/s (range, 0.0–33.8), with 75% within 1 m of the water's edge. Fathead minnow (n = 164), white sucker (*Catostomus commersonii*; n = 62), and mosquitofish (*Gambusia affinis*; n = 33) were found in deeper water and higher velocity than were RGSM, and only common carp (n = 142) were found in shallower water (Figure 8). No RGSM larvae were collected in open water, and all were associated with vegetative cover, including woody (65%), herbaceous (35%), and aquatic (0.3%) vegetation (Figure 9). Mosquitofish were found in similar cover as RGSM, and the four other species were also associated with vegetative cover, although fathead minnow, common carp, and white sucker were found in open water.

An analysis of covariance showed that of six covariates (site, date, depth, velocity, distance to water's edge, and cover type), proximity to

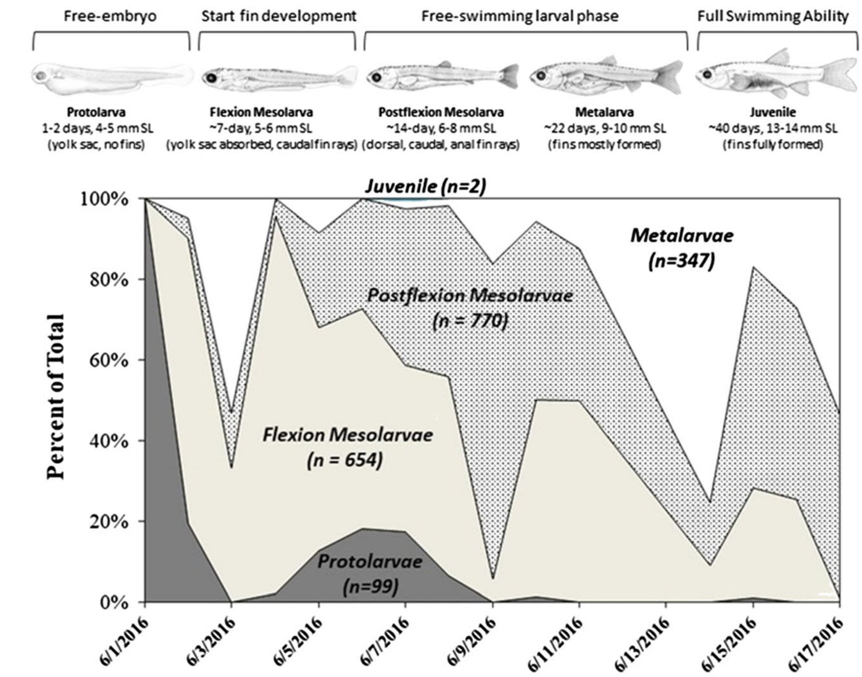

FIGURE 7 Cumulative daily proportions of larval phases of Rio Grande silvery minnow collected June 1–17, 2016, from six restoration sites of the Middle Rio Grande (n = 1,872). Overlay with illustrations and lengths of larval and juvenile Rio Grande silvery minnow from Brandenburg (2018), and estimated ages of developmental phases from Platania and Dudley (2003). ABCWUA, Albuquerque Bernalillo County Water Utility Authority

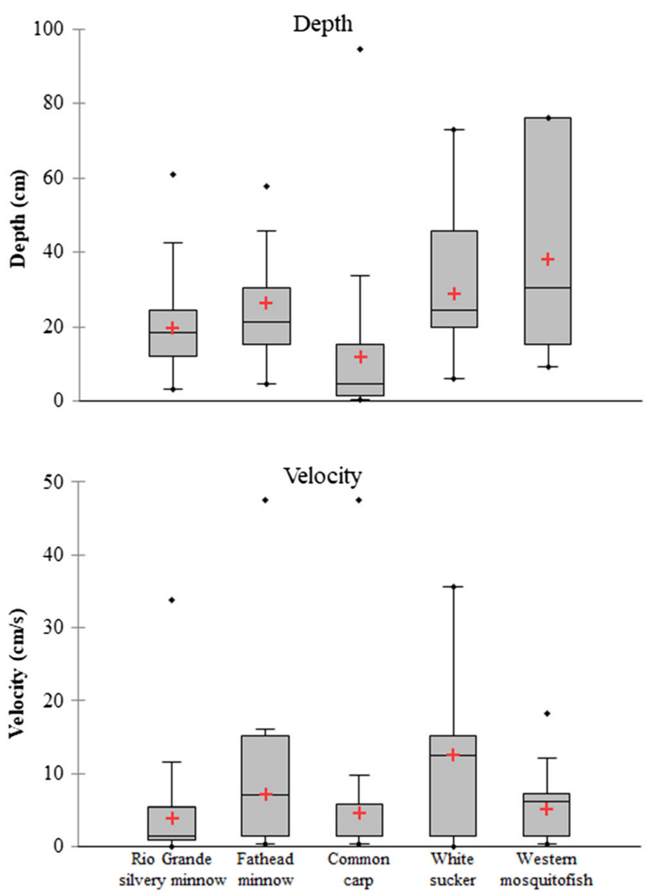

FIGURE 8 Depth and velocity of dip net locations occupied by the most common species of larval fish in the six restoration sites. Variables are weighted by numbers of fish at each sample location

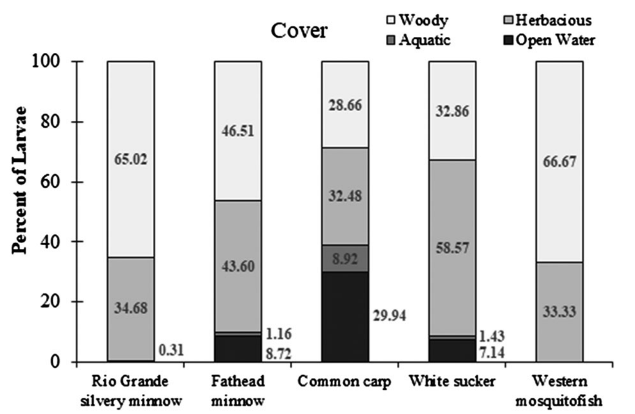

FIGURE 9 Percentage of larvae captured in dip nets from specific cover types

the water's edge of <1 m was the only significant effect (p = .0144–.0001) on count of larval RGSM at dip net locations, except for the Willie Chavez North site, which yielded the lowest larval count (20) and CPUE (0.1 fish/dip net). The analysis of covariance for all sites combined also showed that although the effect of edge was most significant (p < .0001), the date of collection (p = .1961), cover type (p = .229), and site (p = .3171) also affected larval counts by dip net location, though not significantly (Table 5).

4 | DISCUSSION

Floodplain formation in the MRG is important in maintaining the wooded riparian corridor (bosque) and large cottonwood gallery for which the river is known (Molles et al., 1998). Inundated riverside depressions, side channels, and floodplains support a variety of species, including the endangered RGSM (Pease et al., 2006), but poor runoff can preclude overbank flooding in some years (Magaña,

TABLE 5 Analysis of covariance for six source variables correlated to number of Rio Grande silvery minnow captured with dip nets in six restoration sites

Source	*DF*	*SS*	*MS*	*F*	*p*
Date	10	590.8	59.08	1.36	.1961
Depth	3	16.7	5.56	0.13	.9436
Velocity	2	7.6	3.82	0.09	.916
Cover	3	188.4	62.8	1.44	.229
Edge	1	5,506.4	5506.43	126.63	<.0001
Site	1	43.6	43.6	1	.3171
Error	542	23,567.8	43.48	—	—
Total	562				

2012). The relationship of spring runoff to the RGSM population is not well understood, but Archdeacon (2016) advised that managers focus on providing spring flows in the MRG and prevent three consecutive poor spring runoff years to prevent potential RGSM population collapse. This study indicates that spring runoff of sufficient magnitude and duration is necessary to provide habitat for spawning, egg incubation, and larval nursery that lead to successful annual survival and recruitment.

Since 2003, the MRGESCP has restored floodplains and other low-lying riverside areas of the MRG to promote more frequent inundation at lower discharge, and water managers coordinate regularly to manage reservoir storage and day-to-day operations in balance with natural resource needs. Interannual and intraannual discharge of the MRG is highly variable, and there is limited flexibility for water management; hence, maximum benefit of available water must be gained from an in-depth scientific understanding of the relationship between river discharge and natural resources, including the RGSM.

4.1 | RGSM use of floodplains

All life stages of the RGSM have been found in floodplains of the MRG, including eggs, larvae, juveniles, and adults, as compelling evidence that these inundated riverside habitats are important for spawning, egg incubation, and larval nurseries (Gonzales et al., 2014; Magaña, 2012; Medley & Shirey, 2013; Pease et al., 2006; Tave et al., 2018). In May–June of 2008–2009, Gonzales et al. (2014) reported adult RGSM as 80% (n = 11,602) of overall catch and red shiner as 16% in MRG floodplains. In our study of May–June 2016, adult RGSM were the second most common species in restored floodplain sites with 18% (n = 127) of total catch and red shiner comprised 75%. The number of RGSM adults in our study was probably low because of the large interannual variation in abundance, as indexed by the prior annual October census of only 0.16 fish/100 m^2 in 2015, compared with >10 fish/100 m^2 in 2007 and 2008 (Dudley et al., 2016a).

Ripe and gravid RGSM appear and persist in newly inundated floodplains of the MRG in spring, indicating that the species uses these habitats for spawning. During spring sampling, large concentrations of reproductively mature RGSM are often collected on inundated lateral overbank habitats (Hatch & Gonzales, 2008). Of 11,602 adults examined by Gonzales et al. (2014) in 2008–2009 from constructed and natural floodplains of the MRG, 40%, 12%, and 27% were gravid females, spent females, and males expressing milt, respectively, leading them to conclude that spawning activity was likely taking place in floodplains. Large numbers of adults were not available from our study, but of the 127 captured, 13%, 9%, and 14% were gravid females, spent females, and males expressing milt, respectively, which also indicate active floodplain spawning in 2016. The evidence that the species is a floodplain spawner is further supported by studies in an outdoor aquaculture facility (Tave & Hutson, 2012), in which RGSM adults left the stream during hydrological manipulation and entered off-channel, low-velocity habitats where they spawned exclusively (Hutson et al., 2018). Medley and Shirey (2013) examined the characteristics of RGSM eggs and proposed that the species is primarily a demersal floodplain spawner with evolved eggs that are secondarily buoyant in high sediment environments rather than a main channel pelagic, broadcast spawning species with an evolved long-distance downstream drift phase.

Large numbers of adult RGSM in floodplains of the MRG (Gonzales et al., 2014; Hatch & Gonzales, 2008) and the results of controlled studies in an aquaculture facility (Hutson et al., 2018) also indicate a concerted lateral movement by adults from the mainstem to newly inundated habitats, where most appear to remain, or move in and out, throughout inundation. Movement of adults to floodplains has also been observed for the related eastern silvery minnow (*Hybognathus regius*; Raney, 1939). This is an observed phenomenon in other rivers with fishes seeking sheltered productive habitats for spawning and feeding (Junk, Bayley, & Sparks, 1989), including rivers such as the Mekong River in China (Baran, Van Zalinge, & Ngor Peng, 2001), the Jamuna River in Bangladesh (de Graaf, 2003), and the Kankakee River in Illinois (Kwak, 1988), where notable upstream and lateral movements of fish to inundated floodplains occur with increased discharge as fish move to spawn in nutrient-rich waters. A longitudinal spawning-related movement by RGSM has not been detected in the MRG, but the large numbers of ripe and gravid adults in floodplains indicate a substantial lateral movement from the mainstem to newly formed riverside floodplains where abundant eggs and larvae indicate in situ spawning.

4.2 | Time of spawning for RGSM

4.2.1 | Role of photoperiod, temperature, and discharge

Knowing when RGSM spawn in the MRG is important for understanding how timing, magnitude, and duration of runoff affect spawning, nursery habitat, and reproductive success. The onset of RGSM spawning in the wild is not well understood but appears to be driven by a set of complex factors that include season, water temperature, and river discharge (USFWS, 2010). The synergistic effect of increased photoperiod and temperature in spring typically induces oocyte development in fishes (de Vlaming, 1975) and appears to lead to gonadal maturation of female RGSM in the wild, but the onset of spawning is apparently cued by a hydrological event. Platania and Dudley (2008) reported that spawning by RGSM appeared to be strongly associated with changes in flow and water temperature. More recently, Hutson et al. (2018) determined from an outdoor aquaculture facility that the most important spawning cue for RGSM appeared to be an increase in flow stage during the spring snowmelt runoff. That change in stage may be the increased discharge that leads to floodplain inundation or a flow spike prior to or absent of inundation.

The distribution of hatching dates from this study indicates that female readiness and spawning are not simultaneous across the population and that different females are at different stages of gonadal maturation and cued by different sequential hydrological events. This phenomenon was observed with changes in environmental flows that enhance native fish spawning and recruitment in the Murray River, Australia (King, Tonkin, & Mahoney, 2009). Similarly, spawning peaks of the large river cyprinid Colorado pikeminnow (*Ptychocheilus lucius*) were associated with flow spikes of the Yampa River, Colorado (Nesler, Muth, & Wasowicz, 1988). Individual RGSM in laboratory trials have been observed in multiple spawning events of 3–18, with 15–30 min between events (Platania & Altenbach, 1996), but this probably does not account for the spatial distribution in spawning and hatching dates observed in our study.

4.2.2 | A predictor of spawning time

A predictor of spawning time for RGSM is needed to explore hydrological opportunities that will enhance spawning, egg incubation, and nursery habitat. As a first approximation of a temperature index, we computed cumulative mean daily river temperature at the Alameda Bridge of 717 and 692 ACDDs for the start of spawning in the Angostura and Isleta reaches, respectively. No other estimates of ACDDs are available for RGSM spawning, which are among the earliest of spawning cyprinids in the MRG (Krabbenhoft et al., 2014). Comparable estimates of growing season degree-days (synonymous with ACDDs) for the start of spawning by the congeneric brassy minnow (*Hybognathus hankinsoni*) was 671 (April 25) in the Arikaree River, Colorado, and 741 (April 30) for the fathead minnow (Falke et al., 2010). Computed ACDD was 758 (June 1) for the red shiner and 727 (May 30) for the fathead minnow in the Yampa River, Colorado, based on 1981 spawning dates by Muth and Nesler (1993). These studies show that spawning dates and ACDD for a species can vary and are each best represented by a range of values.

The ACDDs derived for RGSM from our study probably reflect photoperiod and temperature accumulation, as well as a hydrological spawning cue; daily increases in discharge of 200–300 ft^3/s (5.7–8.5 m^3/s) occurred in early and middle April, correspondent with the onset of spawning (see Figure 5). A more resolute predictor of gonadal maturation by RGSM in the MRG is necessary and can be derived as a measure of cumulative degree-days for fish in captivity (e.g., Chezik et al., 2014; Kuo, Nash, & Shehadeh, 1974) and confirmed by sampling wild fish for gonadosomatic index (Platania & Altenbach, 1996; Rheman, Islam, Shah, Mondal, & Alam, 2002). This predictor will allow managers to know when the fish are ready to spawn so as to synchronize discharge with spawning and larval hatch, as hydrological conditions allow.

4.3 | Residence time of larvae in floodplains

The amount of time that RGSM larvae need to remain in floodplains is important in understanding the duration of floodplain inundation necessary for maximizing larval survival. Our observations of the temporal occurrence of developmental larval phases in MRG floodplains indicate that residence time is linked to ontogenetic development and swimming ability.

4.3.1 | Swimming ability of RGSM larvae

Newly hatched RGSM larvae are altricial with little swimming ability and a need for quiet, sheltered, productive habitats for feeding and escaping predators, until they are sufficiently developed and able to swim. The swimming ability of larval fishes improves with developmental phase and is linked to fin-ray development and muscular coordination, as shown in swimming performance studies of species that undergo similar ontogenetic development as RGSM (e.g., Fisher, Leis, Clark, & Wilson, 2005; Kopf, Humphries, & Watts, 2014; Voesenek, Muijres, & van Leeuwen, 2018). Most larval fishes undergo three principal developmental phases, including protolarva, mesolarva (including flexion and postflexion subphases), and metalarva, before transforming to juveniles (see Figure 7).

The RGSM in the newly hatched protolarval phase is about 4 mm long and characterized by a yolk sac, fin folds, and an absence of fin rays. Mobility is limited, and the larvae reposition to feed and escape predators by performing a “C-start,” where they curl their body into a C-shape and then uncurl to generate thrust and acceleration (McGee et al., 2009). Flexion mesolarvae are about 6mm SL and have a beginning but incomplete complement of principal caudal-fin rays. Their mobility is limited to the C-start strategy and by an absence of most fin rays, but internal physiological myomere development provides some coordinated movement (Voesenek et al., 2018). Postflexion mesolarvae are about 7mm SL and characterized by an adult complement of principal caudal-fin rays and development of dorsal- and anal-fin rays, but no pectoral- or pelvic-fin rays. This and the development and restructuring of the axial muscle system enable the fish to exhibit coordinated swimming mobility, but the absence of paired fin-rays limits stability in current and for foraging (Voesenek et al., 2018). The fish transform into the metalarval phase at about 9mm SL and are characterized by a full complement of principal rays in all median and paired fins, which gives individuals full mobility. The transformation from metalarvae to juvenile is characterized by a fully developed complement of fins and fin rays (Brandenburg, 2018), along with the development of a fully coordinated musculature that increases swimming efficiency (Voesenek et al., 2018).

Swimming performance studies of larval RGSM have not been conducted, but studies of other larval riverine fishes shed some light on the development of swimming ability. Studies of larval fishes from Australia's Murray–Darling river found that developmental phase better explained swimming ability than length, size, or age, as critical speed of six riverine species was fastest as metalarvae, with prolonged maximum speed ranging from 1.1 cm/s for silver perch (*Bidyanus bidyanus*) to 15.4 cm/s for trout cod (*Maccullochella macquariensis*; Kopf et al., 2014). Batty and Blaxter (1992) also found improved swimming performance with development, as newly hatched larvae of herring (*Clupea harengus*) swam at 8–15 cm/s and late-stage larvae at 10–16 cm/s. Prolonged swimming speeds of larval robust redhorse (*Moxostoma robustum*) in the Oconee River, Georgia, were 6.9 and 11.7 cm/s for early- and late-stage larvae 13.1 and 20.4 mm long, respectively (Ruetz & Jennings, 2000). Increased swimming performance in the later larval phases is consistent across species, including coral reef fishes (Fisher et al., 2005).

The swimming ability of larval RGSM is not known but is probably within the range of other larval fishes. Larval RGSM in MRG floodplains were found at a mean velocity of 3.9 cm/s and a mode of 1.5 cm/s, which are within the range of swimming ability for other larval species and the likely range of RGSM. The velocity range of all dip net locations was 0–60 cm/s, which indicates that pockets of low velocity exist where postflexion mesolarvae and metalarvae can maneuver throughout a floodplain site and possibly intentionally or inadvertently depart the site in search of food or to escape predators. Swimming performance studies of larval RGSM are needed to better understand the developmental phase at which the larvae are capable of surviving outside of floodplain habitats and to evaluate the habitat features of floodplains that provide suitable velocity conditions.

4.3.2 | Departure of larvae from floodplains

Swimming performance studies and our observations of developmental phases indicate that RGSM larvae reach a sufficient level of development and mobility as postflexion mesolarvae (~14 dph) and metalarvae (~22 dph) that enable individuals to more actively seek prey and escape predators outside of a floodplain environment. This time frame is consistent with observations at an outdoor aquaculture facility, where RGSM “fry” actively moved from simulated floodplains into the stream channel 2.5 weeks post spawn (Hutson et al., 2018). We found no evidence of a mass exodus of larvae or juveniles from MRG floodplains triggered by flow or temperature, and their departure appeared to be gradual as individual fish reached the later phases of development. Departure from floodplains may also be prompted by the growing larvae in search of more and larger food items (see Section 4.5).

The managed runoff of 2016 was of sufficient duration to allow many RGSM to mature past the larval stage within the floodplain sites, but only two of 1,838 larvae collected were juveniles, leading us to believe that the fish departed gradually and voluntarily in the later larval phases. It appears that as long as a floodplain site is inundated and suitable conditions of cover and food persist, RGSM larvae will remain resident through most of their larval stage, with individuals capable of departing as postflexion mesolarvae and metalarvae (14–22 dph) and by their transformation to juveniles (~40 dph).

4.4 | Synchrony between hatching and runoff

We projected the presumed residence time of 14 and 22 days for individual RGSM larvae in floodplains to illustrate the correspondence of hatching times with the increase in river discharge and the duration of floodplains inundation for 2016 (Figure 10). The managed runoff enabled discharge to remain above 1,500 ft^3/s for 35 continuous days (May 17 to June 20) and provided nursery habitat for the newly hatched larvae from just past the peak of hatching in the Angostura reach (May 11) to about 2 weeks after the latest hatch date (June 3). The earliest hatched fish of mid-April to mid-May were likely spawned in the mainstem and mostly transported downstream in the absence of floodplains, although some were probably retained in floodplains that inundated at lower discharge or along irregular shoreline features, as demonstrated by drift of artificial eggs (Widmer et al., 2012). Most RGSM hatched after mid-May were probably spawned in the floodplains or in the main channel and entrained in floodplains as eggs or larvae.

On the basis of the estimated number of larvae hatched by date in 2016, about 70% were hatched before floodplain inundation and 30% during inundation. Had the runoff occurred 2 weeks earlier, virtually all of the hatched larvae would have had access to floodplain habitat from hatching through 14- or 22-day individual residence times. Loss of earliest hatched fish from the system may explain the small number of larvae at the beginning of the hatch and the apparent normal distribution of hatch times; possibly, larger numbers were hatched early and did not survive or become entrained in the floodplains sampled.

Ideally, floodplain inundation should start with, and possibly trigger, the onset of RGSM spawning so that the newly hatched larvae have immediate access to sheltered, productive habitats. Inundation should persist throughout the period of hatching so that each larva can remain in a floodplain for 14–22 days. In 2016, this time period was about 1.5–2.0 months for the 53-day period of hatching (Figure 10). This scenario is unlikely in all but the wettest years, when a long period of inundation happens to coincide with spawning. In most years, runoff and floodplain inundation are probably out of synchrony with spawning, and reproductive success depends largely on the proportion of hatch in the presence of floodplains. In years with low runoff, a shortened inundation period is likely to partially desiccate or drain the floodplain before the larvae reach a sufficient level of development and result in stranding with low survival and poor recruitment. Larval survival will depend on developmental phase, with higher survival occurring in the later phases as individuals are able swim with receding flows and cope with more rigorous environments outside of floodplains. Larval survival and recruitment are likely to be enhanced when nursery floodplain habitat is available for a greater proportion of the hatch.

4.5 | Floodplain features used by larval RGSM

4.5.1 | Depth, velocity, and cover

We found large numbers of larval fishes in restored sites of the MRG, with RGSM comprising 73% of all larvae collected. The RGSM larvae were found in shallow depth (19.6 cm) and low velocity (3.9 cm/s),

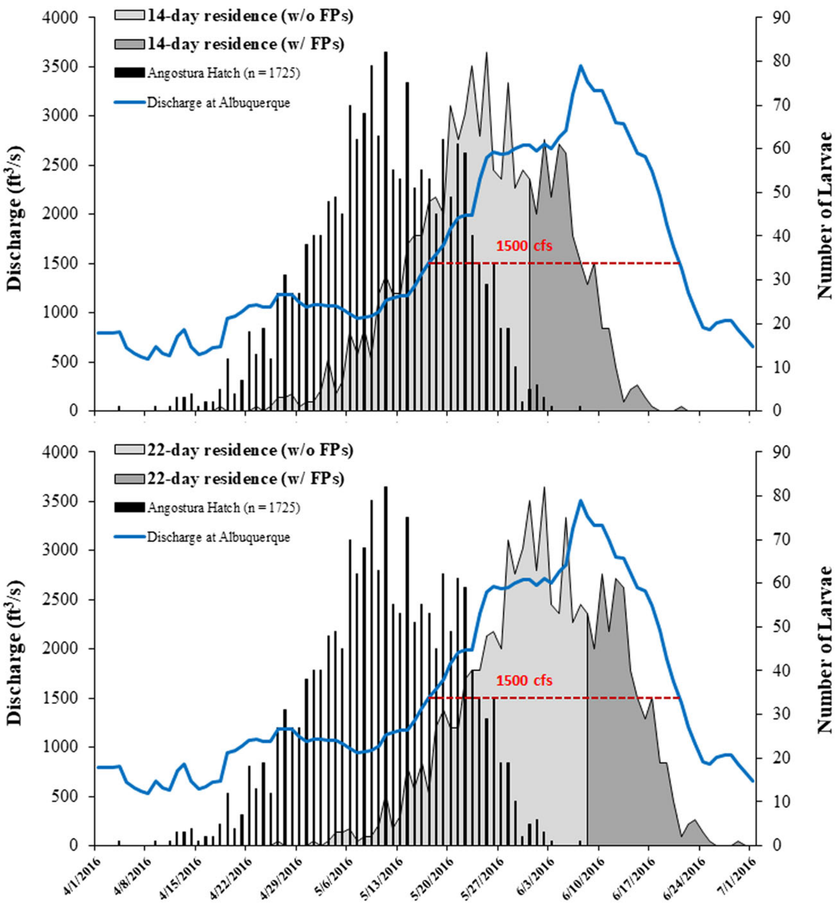

FIGURE 10 Estimated hatch dates of Rio Grande silvery minnow and the projected end of floodplain residence by larvae for 14 and 22 days, divided as larvae hatched with and without floodplains (FPs). Discharge is for the Rio Grande at Albuquerque (U.S. Geological Survey #08330000). Horizontal dashed line shows discharge of 1,500 ft^3/s where inundation of the six study sites began

similar to findings of other studies in the MRG (Magaña, 2012; Pease et al., 2006). No clear distinction in habitat characteristics could explain the observed differences in fish catch in each site. It was also difficult to characterize microhabitat conditions because of constantly changing river conditions; however, an assessment of vegetative cover at the sites with the highest RGSM CPUE had 45–86% terrestrial wood vegetation, 0–13% herbaceous vegetation, and 0–45% open water. This suggests that some form of vegetative cover is important for RGSM possibly to reduce predation risk, private forage opportunities, or both, but the type of vegetation did not appear to matter. Other cover types, such as leaf litter, woody debris, and tumble weeds, were also present in small amounts but were not disproportionately used by the larvae. Observed behaviour of RGSM in an outdoor aquaculture facility included schooling and the use of vegetation for cover and predator avoidance (Tave et al., 2018). The association of larval fish with cover is common to many fish species in other river basins. In the Mekong River, the diversity and abundance of fishes in floodplains were related to the diversity of habitats, where flooded forests harboured more species than flooded grassland, and barren lands were virtually free of fish (Baran et al., 2001).

4.5.2 | Chronology of food production

Proximity to the water's edge was the only significant effect (p = .0144–.0001) on count of larval RGSM in dip net locations. We found 75% of RGSM larvae within 1 m of the water's edge and usually in association with a green or yellow green band of periphyton. This phototrophic band of periphtyon develops within 2 days of inundation and includes algae, diatoms, and small insects (Valdez, Beck, Medley, Schmidt-Petersen, & Zeiler, 2015). Rich detritus, diatoms, algae, and invertebrates are important food sources for larval RGSM (Watson, Sykes, & Bonner, 2009), and the timing of their appearance in these floodplains is critical to larval survival. Larvae of RGSM assimilate their yolk sac at 5mm SL (Brandenburg, 2018), or about 3–7 dph, and they undergo a "critical period" when nutrition shifts from endogenous (yolk) to exogenous (diatoms, algae, zooplankton) sources. At this time, the larvae require immediate sources of moderate to high food densities to avoid starvation, as observed for other floodplain species, such as the razorback sucker (*Xyrauchen texanus*; Papoulias & Minckley, 1990).

Food of the size proportional to the mouth gape of a fish is important, especially for first-feeding larvae. Larval fish often suffer prodigious mortality rates during the transition from endogenous reliance on their yolk sac to exogenous food items. Most fish feed by creating a vacuum and sucking their prey into their mouth. The youngest larvae have small mouths that impede suction feeding performance if the food is too large, reducing feeding success and feeding rate, ultimately resulting in "hydrodynamic starvation" in first-feeding larvae (Holzman et al., 2015). The synchrony of floodplain formation in the MRG with hatching of RGSM larvae is vital not only for the availability of sheltered habitat but also for the appropriate kinds and sizes of food items.

In floodplains of the MRG, as in floodplains of other rivers, a surge in primary and secondary production is characteristic of newly inundated floodplains (Magaña, 2012; Pease et al., 2006), and the synchrony between this onset of production and the appearance of larval fish is vital to early life-stage survival (Baran et al., 2001; Welcomme, 1985). Most floodplains produce an abundance of food for fish in the first weeks of inundation, although the amount of production may vary with floodplain site (Gourley & Crowl, 2002). Production in floodplains occurs as a chronology of communities that begins with an appearance of rich detrital loads, algae, and diatoms shortly after inundation. This is followed by the emergence of various forms of zooplankton, such as rotifers and copepods, and then by larger forms including cladocerans and various insect larvae (Baranyi, Hein, Holarek, Keckeis, & Schiemer, 2002; Crowl, Gourley, & Townsend, 2002; Mabey & Shiozawa, 1993). Watson et al. (2009) found that small RGSM (9 to 20mm total length) in outdoor ponds consumed a greater variety of food than did larger fish and that food items were primarily insects, diatoms, cladocerans, rotifers, filamentous algae, bryozoans, and copepods that had developed as part of the production cycle of the ponds; these food items were also utilized by larger RGSM and can provide energy for adults in floodplains during and after spawning.

Given that MRG floodplains are ephemeral and short-lived for usually <60 days, a more mature invertebrate community with mayflies, damselflies, and caddisflies may not become established, possibly forcing the larger larval RGSM to move outside of the floodplain where larger food items are available (Valdez et al., 2015). Because productivity in these floodplain sites is reset every year, it is important to understand the dynamics of the periphyton and planktonic communities as affected by the topography and cover of constructed floodplain sites in synchrony with river discharge.

5 | CONCLUSIONS

1. This study investigated the mechanisms associated with the positive relationship between spring river discharge and RGSM CPUE, which is the fundamental principle for the “production strategy” of the 2016 biological opinion (USFWS, 2016). The weight of evidence shows that the relationship is driven by floodplain availability for spawning, egg incubation, and nurseries for larvae. The evidence also shows that larval survival and recruitment are enhanced when spring floodplain inundation is synchronous with spawning and hatching, floodplain inundation encompasses a large proportion of the hatch, individual larvae remain in floodplains 14–22 days, vegetative cover is sufficient for larvae to feed and escape predators, and a periphyton and planktonic food base is abundant in newly inundated floodplains.
2. The managed runoff of 2016 contributed to the highest RGSM density since 2009, with a CPUE for all ages (99% age 0) of 7.20 fish/100 m^2 in October 2016, compared with 0.16 in 2015 (Dudley et al., 2016a). Although floodplain inundation above 1,500 ft^3/s occurred for only 30% of the hatch, survival and recruitment were sufficient to substantially increase population density. The managed flow may not be the singular cause of the higher CPUE, but persistent summer flow may have also contributed.
3. The information gleaned from this study shows that small shifts in timing of runoff in the MRG can make a big difference in providing necessary floodplain habitat for larval RGSM, as hydrological conditions allow. A predictor of gonadal maturation for female RGSM will help managers synchronize river discharge, when possible, to provide the maximum benefit for larval survival and recruitment. This type of cued hydrological management strategy is being used in the Green River, Utah, to provide inundated nursery floodplain habitat for the endangered razorback sucker by using larval occurrence as a trigger for releases from Flaming Gorge Dam to match the peak flow of the tributary Yampa River (Patno et al., 2012).
4. Despite the complex water delivery network of the MRG, this study shows that temporary storage and release of water from upstream reservoirs, such as El Vado, can enhance the magnitude and duration of spring runoff sufficient to make a measurable difference in the RGSM population by providing inundated floodplain habitat for spawning, egg retention, and larval rearing. Section 1174 of America's Water Infrastructure Act of 2018 authorizes the Secretary of the Army to restore peak flow in the MRG by restarting the temporary deviation in the operation of Cochiti Lake and Jemez Canyon Dam and provides another possible option for managing spring runoff in the MRG.
5. The managed runoff of 2016 demonstrated how coordination among federal, state, and local agencies can benefit an endangered species. Under the right conditions, flow modification can be one of the water management tools that do not rely on a permanent conservation pool and do not require using water from agriculture and municipalities. Depletions due to the managed runoff must be addressed but are a relatively small cost, compared with purchasing water for permanent pools.
6. This study provided a retrospective analysis of the relationship between floodplain inundation and time of RGSM spawning that can set the stage for an adaptive management strategy of evaluating the effect of condition-dependent flows on nursery habitat formation and reproductive success and recruitment for the endangered RGSM.

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ORCID

Richard A. Valdez https://orcid.org/0000-0002-2067-8500

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