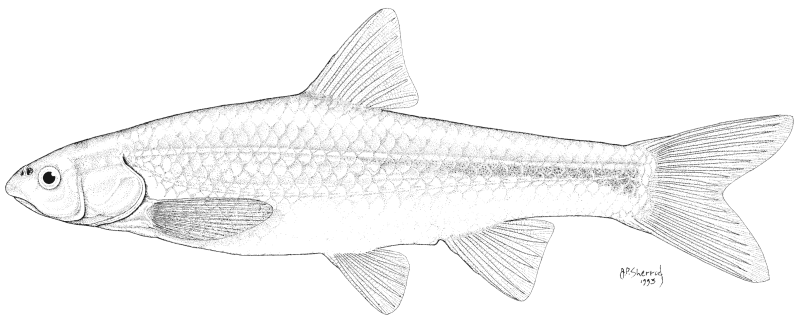
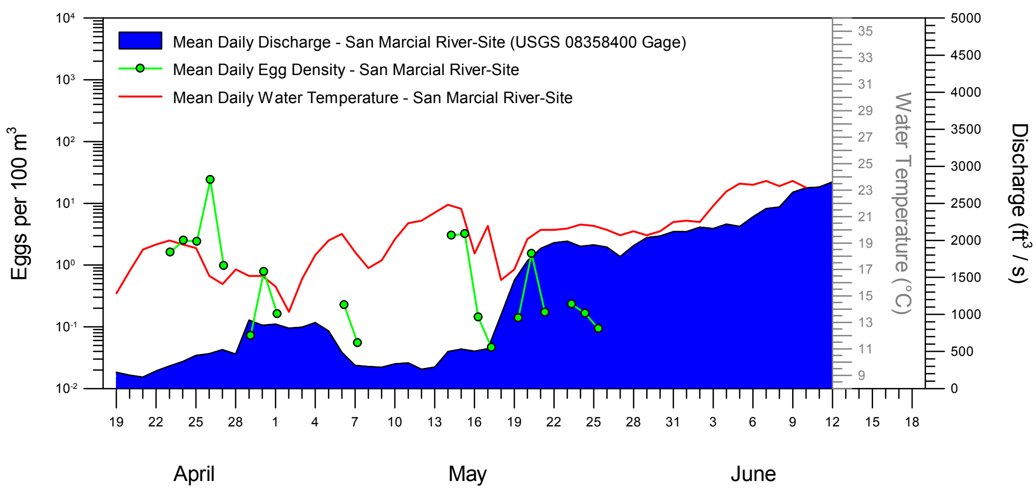
Rio Grande Silvery Minnow Reproductive Monitoring during 2016 in the Rio Grande and Selected Irrigation Canals

A Middle Rio Grande Endangered Species Collaborative Program Funded Research Project





Robert K. Dudley[1], Steven P. Platania[1], and Gary C. White[1,2]

[1] American Southwest Ichthyological Researchers, L.L.C.
800 Encino Place NE; Albuquerque, NM 87102-2606
&
[2] Department of Fish, Wildlife, and Conservation Biology
239 Wagar; Colorado State University; Fort Collins, CO 80523-1474

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U.S. Bureau of Reclamation
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555 Broadway NE, Suite 100
Albuquerque, NM 87102-2352

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

EXECUTIVE SUMMARY

Systematic monitoring of the reproduction of Rio Grande Silvery Minnow has been conducted annually since 2001. Previous studies demonstrated mid-April to mid-June as the primary period of spawning activity. The 2016 study was a continuation of the long-term monitoring effort in the downstream-most river reach, just upstream of Elephant Butte Reservoir. Additionally, five upstream sites (three in the Isleta Reach and two in the San Acacia Reach) provided data on the entrainment of Rio Grande Silvery Minnow eggs into the Middle Rio Grande irrigation canal network since 2013.

Rio Grande Silvery Minnow mixture-model estimates ($E(x)$), using standardized egg passage rate data (E_p = eggs / s) from 2003–2016, were highest in 2011 (5.40×10^1) and lowest in 2004 (9.62×10^{-4}). Values of E_p are indicative of the relative downstream transport of eggs across years, corrected for annual differences in flow magnitude. There was a steady decline in estimated egg passage rates from 2011–2013, followed by an increase in 2014. Egg passage rates declined ($P < 0.05$) from 2015 (7.05×10^{-1}) to 2016 (4.91×10^{-2}).

General linear models of Rio Grande Silvery Minnow mixture model estimates revealed that variation in the mean of the lognormal distribution of E_p (μ) and the probability of occurrence (δ) was reasonably predicted by changes in hydraulic variables (allowing for random effects) over time (2003–2016). The top model (δ(Year) μ(SANmax+R)) received about 37% of the AIC_c weight (w_i). The next two models, which accounted for about 42% of the cumulative w_i, were related to the interaction among δ, μ, and hydraulic variables representing persistently low flows. The global model (δ(Year) μ(Year)) received only 6% of w_i, and nearly all remaining model combinations (197 out of 200) received < 1% of w_i. High peak flows were associated with decreased egg passage rates, while extended low flows were associated with increased egg passage rates.

Logistic regression modeling of Rio Grande Silvery Minnow egg presence-absence data revealed strong associations with the percentage change in mean daily discharge just prior to egg collection (X^2 = 34.79 and $P < 0.001$). The probability of collecting eggs was predicted to increase rapidly up to about a 100% increase in mean daily discharge between days just prior to egg collection. The probability of collecting eggs during a 100% increase in flow was 0.83 and during a 200% increase was 0.97.

While Rio Grande Silvery Minnow eggs were collected at only one of the three canal-monitoring sites during 2016, eggs were documented at all three river-monitoring sites. The mixture-model was used to estimate the egg passage rate at the Isleta (0.06), San Acacia (0.06), and San Marcial (0.06) river-sites; there were no differences ($P > 0.05$) among these estimates. The estimated egg passage rate at the Isleta river-site was higher ($P < 0.05$) than at the Belen (0.0) or Peralta canal-sites (0.003). The estimated proportion of eggs entrained and water diverted in the Isleta Reach was 0.05 and 0.18, respectively. However, the estimated egg density at the Isleta river-site was not different ($P > 0.05$) from the estimated egg density at the two canal-sites combined. The estimated egg density and passage rate at the San Acacia river-site was higher ($P < 0.05$) than at the Socorro canal-site. The estimated proportion of eggs entrained and water diverted in the San Acacia Reach was 0.0 and 0.0, respectively.

Despite the seemingly large number of Rio Grande Silvery Minnow propagules transported downstream every year, some portion remains upstream. The physical conditions produced by prolonged and elevated flows during spring result in overbank flooding of vegetated areas, formation of inundated habitats within the river channel, and creation of shoreline and island backwaters. It is likely that the proportion of individuals retained and successfully recruited upstream is related to the complexity of instream habitat conditions and the long-term availability of nursery habitat. Since successful growth and survival of Rio Grande Silvery Minnow from the egg through the early larval stages requires at least three weeks, the persistence of these nursery habitats is essential during this critical phase of development.

While Rio Grande Silvery Minnow has declined markedly throughout its range since 2009, the improved spring runoffs of 2015 and 2016 resulted in decreased egg passage rates as compared with 2014. However, the recruitment success of this species during the fall of 2016 will likely be highly dependent on summer flow conditions. The loss of individuals from downstream reaches during river drying events is particularly pertinent, as the occurrence and density of this species is consistently higher in these vulnerable areas. The future conservation status of Rio Grande Silvery Minnow appears strongly dependent on reliably ensuring appropriate seasonal flow and habitat conditions to support the crucial spawning and early recruitment phases of this species.

INTRODUCTION

The reach of the Rio Grande between Cochiti Dam and Elephant Butte Reservoir (Middle Rio Grande) has been greatly modified over the last 50 years; this has alternatively led to aggradation, degradation, armoring, and narrowing of the river channel in different portions of the reach (Lagasse, 1985). This section of the river flows through the massive Rio Grande rift and historically resulted in a wide floodplain within the sparsely vegetated Rio Grande valley. Extensive braiding of the river through the relatively linear Rio Grande rift valley was common as it flowed over shifting sand and alluvium substrata; flow in the Middle Rio Grande was generally perennial except during times of severe or extended drought (Scurlock, 1998).

Historically, the Middle Rio Grande was relatively shallow throughout most of the year because of regionally low precipitation levels (Gold and Denis, 1985) but was subjected to periods of high discharge. Flows were generally highest during the annual spring snowmelt runoff (April–June). However, intense localized rainstorms (monsoonal events that generally occur in July and August) often caused severe flooding and were important in maintaining perennial flow throughout the summer. The cyclic pattern of drought and flooding over mobile substrata likely helped to promote the active interaction between the river and its floodplain. Historically, the Middle Rio Grande was characteristic of a dynamic semi-arid river ecosystem.

The reduced species diversity typical of semi-arid ecosystems was also reflected in the depauperate ichthyofaunal composition of the Middle Rio Grande. Despite the reduced overall species richness of the Rio Grande, the river supported numerous native cyprinids that were endemic to this drainage (Platania and Altenbach, 1998). However, many of the endemic pelagic-spawning cyprinids that historically occupied the Rio Grande basin have been extirpated from large portions of their range (Speckled Chub, *Macrhybopsis aestivalis* and Rio Grande Shiner, *Notropis jemezanus*) or have become extinct (Phantom Shiner, *Notropis orca* and Rio Grande Bluntnose Shiner, *Notropis simus simus*) over the past century (Bestgen and Platania, 1990). Rio Grande Silvery Minnow, *Hybognathus amarus*, is the only extant pelagic-spawning cyprinid in the Middle Rio Grande (Bestgen and Platania, 1991; Platania, 1991).

This group of pelagic-spawning cyprinids shared several life-history characteristics. All were small (generally < 90 mm SL), short-lived (ca. 2–5 years), fishes that occupied mainstem habitats. In addition to these shared traits, all five species are members of a reproductive guild of pelagic-spawning fishes (Platania and Altenbach, 1998). These fishes spawn non-adhesive eggs that swell rapidly with water and become nearly neutrally buoyant. Spawning is generally associated with increases in discharge, such as spring run-off or summer rainstorms. The eggs expand from about 1.6 mm to 3.0 mm in diameter shortly after spawning and are passively transported by water currents during development. Egg hatching time is temperature dependent; it usually occurs in 24–48 hours between 25 and 30°C and within 72 hours at 20°C (Platania, 2000). Recently hatched larval fish are subject to additional passive transport for several days (ca. 3 to 5 days) until development of the gas bladder.

The 4–7 days necessary for propagules to attain the developmental stage necessary to control their horizontal movements allows for potentially considerable downstream transport of eggs and larvae in the Middle Rio Grande. As has been well documented for other aquatic organisms, it is necessary for some portion of the drifting propagules to settle in appropriate nearby low-velocity habitats or move upstream to maintain viable populations (Speirs and Gurney, 2001). Downstream transport distance of the progeny of Rio Grande Silvery Minnow is dependent on a variety of factors including flow magnitude and duration, water temperature, and channel morphology (Dudley and Platania, 2007). Historically, there were no permanent barriers to upstream dispersal of fishes in the Middle Rio Grande. However, two large dams (Cochiti and Elephant Butte), along with three smaller dams (Angostura, Isleta, and San Acacia), now prevent the upstream movement of fishes and fragment the once continuous range of Rio Grande Silvery Minnow.

Systematic monitoring of the reproduction of Rio Grande Silvery Minnow was first conducted in 1999 and included sampling in all three reaches of the Middle Rio Grande (Platania and Dudley, 2000). This preliminary, yet extensive, monitoring effort involved quantifying the occurrence and passage of eggs from nine sites; spawning was documented from late March to late June of 1999. Limited egg collecting efforts were also conducted at selected sites in the Middle Rio Grande (Platania and Hoagstrom, 1996) and in the Low Flow Conveyance Channel (Smith, 1998, 1999) from 1996 to 1999. These latter samples provided information on spawning during certain times and for specific sites.

A long-term sampling effort was initiated in 2001 to document spawning by Rio Grande Silvery Minnow (Platania and Dudley, 2002) at a new and permanent location (i.e., not sampled from 1996 to 1999), near the downstream terminus of their range. Monitoring also occurred at this site in 2002 (Platania and Dudley, 2003), 2003 (Platania and Dudley, 2004), and 2004 (Platania and Dudley, 2005). Additional monitoring efforts were conducted from 2006 to 2008 (Platania and Dudley, 2006, 2007, 2008) and resulted in the sampling of the Angostura, Isleta, and San Acacia reaches of the Middle Rio Grande. Recent monitoring in these three reaches has been conducted by a variety of organizations, including ASIR, and has occurred annually since 2009.

The primary objectives of this study were to characterize the timing, duration, and magnitude of spawning by Rio Grande Silvery Minnow and to quantify the entrainment of eggs into canals in the Isleta and San Acacia reaches of the Middle Rio Grande. Additional objectives included assessing differences in Rio Grande Silvery Minnow egg passage rates across years; examining the relationships between discharge and spawning; and characterizing spawning patterns from multiple canal and river sites in the Isleta and San Acacia reaches. Long-term monitoring of spawning by Rio Grande Silvery Minnow provides insight to potential factors affecting trends in annual reproduction and provides managers with timely scientific information on which to base natural resource management decisions in the Middle Rio Grande.

STUDY AREA

The principal area of interest in the Middle Rio Grande is the reach between the outflow of Cochiti Reservoir and inflow to Elephant Butte Reservoir; this area encompasses the range of Rio Grande Silvery Minnow in the Middle Rio Grande (Figure 1). Five upstream reservoirs and numerous irrigation diversion dams regulate flow in the Middle Rio Grande. Cochiti Reservoir has been operational since 1973, is located 76 km upstream of Albuquerque, and is the primary flood control reservoir that regulates flow in the Middle Rio Grande. Reach names were taken from the diversion structure at the upstream boundary of that reach of river. There were three sampling sites in both the Isleta Reach (Isleta Diversion Dam to San Acacia Diversion Dam) and the San Acacia Reach (San Acacia Diversion Dam to inflow of Elephant Butte Reservoir).

The reproductive effort of Rio Grande Silvery Minnow was monitored at a variety of collecting localities in the Middle Rio Grande from 1996 to 1999. However, sampling efforts have only been consistently conducted in the downstream-most portion of the San Acacia Reach since 2001. The San Acacia Reach of the Middle Rio Grande is about 56 miles (91 km) long, extending from the apron of San Acacia Diversion Dam to the head of Elephant Butte Reservoir. A wide and braided river channel, sand substrate, high sediment load, and a broad variety of aquatic mesohabitats characterize sections of this reach. Conversely, some segments in this reach are relatively narrow and result in increased water velocity and decreased habitat heterogeneity. The 12-mile (19 km) reach of the Rio Grande downstream of San Marcial Railroad bridge crossing is confined to a channel that is about 50 m wide. Substrate in this segment of the river is predominately sand, and braiding of the channel is uncommon except under conditions of relatively low flow.

Given the downstream drift of eggs, a downstream location was selected for the long-term collecting activities to maximize the number of eggs collected and potentially rescue eggs destined to drift into Elephant Butte Reservoir where, if hatched, larvae would be subjected to a wide array of nonnative predators. The San Marcial river-site was located near the downstream-most portion of the San Acacia Reach (San Marcial [UTM: 305368 E; 3711978 N]). This site was downstream of a U.S. Geological Survey stream gaging station located near San Marcial, New Mexico (# 08358400). In addition to easy accessibility and favorable river conditions (e.g., wide river channel, current being carried through a single river channel, gently sloped banks, and moderate gradient), the only means of vehicle access to this site was gated. This area has been sampled annually from 2001–2004 and from 2006–2016.

Five additional sites have been sampled since 2013 for the purpose of assessing spatial spawning patterns in the Isleta and San Acacia reaches. Sampling sites in the Isleta Reach were located just downstream of Isleta Diversion Dam; two were in the irrigation canals (Belen High Line Canal [UTM: 343352 E; 3862173 N] and Peralta Canal [UTM: 346125 E; 3863303 N) and one was in the river (Isleta [UTM: 345852 E; 3863658 N]). In the San Acacia Reach, both sites were located just downstream of San Acacia Diversion Dam; one was in the canal (Socorro Main Canal [UTM: 324898 N; 3791367 E]) and one was in the river (San Acacia [UTM: 325339 E; 3790503 N]). These additional sampling sites (i.e., Belen, Peralta, and Socorro canal-sites; Isleta and San Acacia river-sites) not only allowed for a more detailed assessment of spatial spawning patterns but also enabled a direct comparison between canal and river monitoring localities in the two downstream-most reaches of the study area.

Diel and seasonal discharge varied greatly during 2015 and 2016, especially in southern reaches of the Middle Rio Grande (Figure 2). There was a general trend of lower flow at downstream locations (e.g., U.S. Geological Survey (USGS) San Acacia Gage [#08354900] and USGS San Marcial Gage [#08358400]) compared to upstream locations (e.g., USGS Albuquerque Gage [#08330000]). During May and June 2016, flows increased to elevated levels that persisted for several weeks throughout the study area. Peak flows in 2016 occurred in June. Flow conditions in 2015 and 2016 included periods of very low discharge after June, particularly in southern reaches. As compared with the generalized historical spring runoff (based on mean daily discharge values from 1973 [Cochiti Dam operational] to 2015), the timing of this event was typical in 2015 and 2016. While the spring flow magnitude was modest and truncated in 2015, it was elevated and extended in 2016.

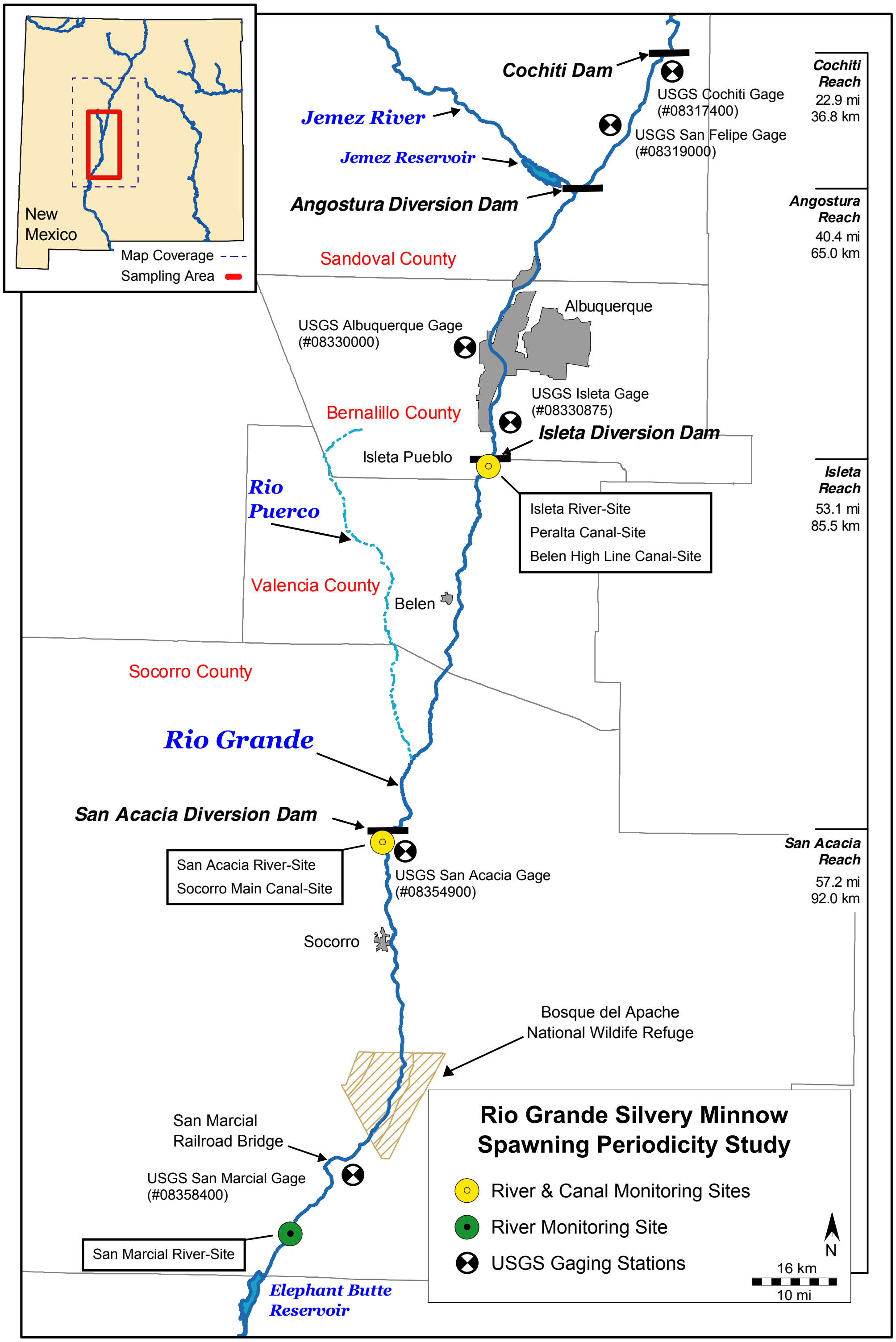

Figure 1. Map of the Middle Rio Grande, New Mexico, and the Rio Grande Silvery Minnow reproductive monitoring sites.

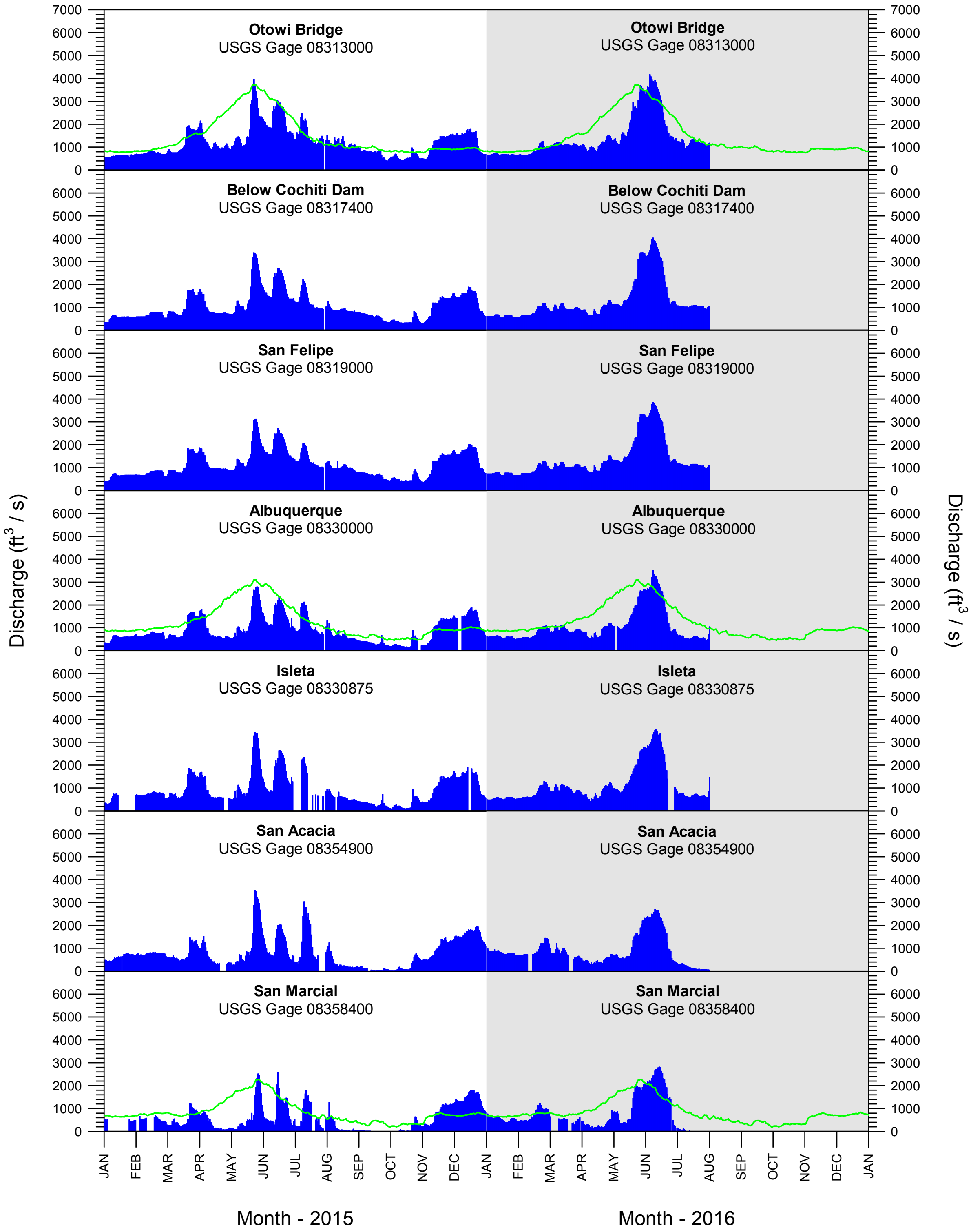

Figure 2. Rio Grande discharge from January 2015 through July 2016 at U.S. Geological Survey (USGS) gaging stations. Green lines are historical mean daily discharge values (from 1973 [Cochiti Dam operational] to 2015). Discharge data are provisional and subject to change.

MATERIALS AND METHODS

The egg-collecting device, developed specifically for the collection of large numbers of live and undamaged semibuoyant fish eggs (Moore Egg Collector; MEC [Altenbach et al., 2000]), was the only sampling apparatus used in this project. We determined the volume of water sampled by using a mechanical flow meter, which was attached to the MEC. The density of drifting eggs (D) was calculated as the total number of eggs (n) collected relative to the total volume of water (V) sampled, using the formula: $D = ((n / V) \cdot 100)$.

Numerous modifications have been made to the collecting gear, since the original publication detailing the construction and operation of the MEC (Altenbach et al., 2000), that have resulted in increased efficiency of the original MEC (i.e., greater volume of water sampled). A modified filtering screen to separate drifting debris from Rio Grande Silvery Minnow eggs was developed and tested for the MEC in 2009. Experimental tests revealed that the modified screen was more efficient at sampling a larger volume of water than was the old screen, but that the egg density estimates were very similar (Platania and Dudley, 2009). Thus, all MECs have been fitted with the modified screen since 2009.

The normal sampling regime consisted of an intensive daily sampling effort at each sampling site. Eggs were not staged (i.e., determining approximate time from spawning), as this would require substantial laboratory work outside of the current core objectives of this study. Staging eggs would give a general idea of drift time but extrapolating to drift distance would be subject to additional assumptions. Two MECs were used at the San Marcial river-site, and one MEC was used at each of the other five sampling sites.

Rio Grande Silvery Minnow egg density values are dependent on flow conditions, thereby precluding unadjusted comparison of inter-annual densities. For example, higher flow volume will result in lower density assuming the number of eggs in the water column remains constant. Egg density (D) was standardized to a downstream passage rate (E_p) based on mean daily discharge (Q) to account for these differences, using $E_p = ((D / 100) \cdot Q)$. Values of E_p (i.e., eggs / s) are indicative of the relative passage rate of eggs across years, corrected for inter-annual differences in flow magnitude. All USGS and MRGCD discharge data presented graphically or analyzed statistically in this report are provisional and subject to change.

Volumetric determination of the number of eggs collected, as employed in 2001, lacked the rigor necessary to evaluate the relative level of spawning. Changes initiated in the 2002 sampling protocol (e.g., direct counts of all eggs collected) were instituted to increase the rigor of the data acquired from this study. However, the continuous sampling protocols employed in 2002, during peak spawning events, were not used in subsequent years. The data collected in 2002 were also highly skewed, making them unsuitable for computing a valid estimate of $E(x)$ (described below). These issues precluded the use of 2001–2002 data for quantitative or statistical comparison with data from subsequent years.

Mixture models (e.g., combining a binomial distribution with a lognormal distribution) have been shown to be particularly effective for modeling ecological data with multiple zeros (White, 1978; Welsh et al., 1996; Fletcher et al., 2005; Martin et al., 2005). Long-term Rio Grande Silvery Minnow spawning data (2003–2016) were analyzed using PROC NLMIXED (SAS, 2016), a numerical optimization procedure, by fitting a mixture model consisting of the binomial and lognormal distributions using the methods outlined in White (1978). Egg passage rate [E_p] and density [D] data, during the most commonly sampled period (1 May to 10 June for 2003–2016 analyses [San Marcial river-site only]; 1 May to 31 May for 2013–2016 analyses [all six sampling sites]), were used for the analysis. Logistic regression was used to model the probability that eggs were collected on any given day, and the lognormal model was used to model the distribution of E_p or D given that eggs were collected. Models provided four parameter estimates for each year (δ = probability of egg occurrence, μ = mean of the lognormal E_p or D distribution, σ = standard deviation of the lognormal E_p or D distribution, and $E(x)$ = estimate of E_p or D). The number of eggs passing a sampling site, during an average 30-day period ($E(x)_{30d}$), was estimated with E_p data by using the formula: $E(x)_{30d} = E(x) \cdot 86{,}400 \text{ s} \cdot 30 \text{ d}$.

General linear models were used to incorporate covariates to model δ, μ, and σ where a logit link was used for δ and log links were used for μ and σ. In the simplest case with no covariates and no random effects, this model can be considered a zero-inflated lognormal model. Covariates considered for modeling spawning data included sampling year (Year) and various hydraulic variables at USGS Gage

#08358400 (SAN; Rio Grande Floodway at San Marcial, NM). Maximum discharge (SANmax), mean discharge (SANmean), and days exceeding threshold discharge values in 1,000 cfs increments (days > 500 [SAN>500], 1,500 [SAN>1,500], and 2,500 [SAN>2,500] cubic feet per second, cfs) were covariates that represented different spring runoff conditions (1 May to 10 June). Days below threshold discharge values (days < 200 [SAN<200] and < 100 [SAN<100] cfs) were covariates that represented different low flow conditions during the same period. Two drought years (2006 and 2013) were excluded from this analysis, as flows never exceeded 100 cfs; more suitable spawning flows occurred only after the termination of sampling. Fixed effects models for each covariate were linear models ($\beta_0 + \beta_1 \times$ covariate) with the corresponding link function. These fixed effects assume that variation in the data is explained by the covariate. That is, for δ, there is no over-dispersion or extra-binomial variation, and for μ, no extra variation provided beyond the constant σ model. Random effects models (*R*) were also considered for δ and μ to provide additional variation around the fitted line, where a normally distributed random error with mean zero and non-zero standard deviation is used to explain deviations around the fitted covariate. Random effects were integrated out of the likelihood (see Pinheiro and Bates, 1995) during fitting of the model.

Goodness-of-fit statistics (logLike = -2[log-likelihood] and AIC_c = Akaike's information criterion [Akaike, 1973] for finite sample sizes) were generated to assess the relative fit of data to various models among all years sampled. Lower values of AIC_c indicate a better fit of the data to the model. Models were ranked by AIC_c values and the top ten models, based on AIC_c weight (w_i), were presented. As environmental covariates were only used to model a single parameter (δ or μ), potential issues of multicollinearity were avoided. Further, AIC_c model selection ranks single-variable models appropriately even if variables are highly correlated (i.e., resulting w_i values would be similar).

Logistic regression was used to determine the relationship between the probability of collecting eggs, based on raw presence/absence data, and the percent change in mean daily discharge from two days to one day prior to egg collection, using long-term sampling data (2003–2016). This was to allow time for the discharge changes occurring at the San Marcial gage to reach the San Marcial river-site (ca. 25 km downstream). This metric best represented the approximate change in mean daily discharge that occurred just prior to spawning. The associated 95% confidence intervals of the modeled regression line were constructed using inverse predictions of discharge across the range of modeled egg collection probabilities (SAS, 2007).

Estimated egg passage rates in the river were compared to those in the canals at similar longitudinal locations, using data collected since 2013. The proportion of eggs entrained into the canals ($E(x)_{EC}$) was computed based on the total of the estimated egg passage rates in the canals ($E(x)_C$) and the total of the estimated egg passage rates from both the river and the canals ($E(x)_{C+R}$), using the formula: $E(x)_{EC} = E(x)_C \cdot E(x)_{C+R}^{-1}$. Similarly, the proportion of water diverted into the canals (Q_{DC}) was computed based on the total of the average discharge in the canals (Q_C) and the total of the average discharge in both the river and the canals (Q_{C+R}), using the formula: $Q_{DC} = Q_C \cdot Q_{C+R}^{-1}$. The average discharge in the river and the canals was calculated based on mean daily discharge values during the study period.

Temperature-logging devices (Onset [Hobo TidbiT v2]) were deployed at each study site to record hourly water temperatures. Data loggers have a published ± 0.21°C level of accuracy over a broad temperature range (0°C to 50°C). The stability (drift) of this device is about 0.1°C per year, but its use was limited to five years. If data loggers became buried in the substrate or were no longer submerged in the water column, corrective measures were taken and invalid data were not included in further analysis. Mean daily water temperature data from canal and river monitoring sites were presented graphically for comparative purposes.

RESULTS

Spawning Periodicity (2003–2016)

Despite substantial inter-annual differences in Rio Grande Silvery Minnow spawning metrics at the San Marcial river-site (Table 1), there were similarities apparent regarding the timing and duration of reproduction over time (2003–2016). Based on the results of data taken from all years of the project, spawning was found to occur in April, May, and June. While the frequency and magnitude of spawning were highly variable across years, the highest numbers of eggs were typically collected during a relatively short period in May. During 2016, mean daily water temperature at San Marcial fluctuated from about 14°C to 22°C in May but consistently remained above 20°C during June.

Mean daily water temperatures during the initial and peak spawning events were relatively similar among years. In general, mean daily water temperatures ranged from about 17 to 22°C during peak spawning events. However, spawning occurred across a wide range of water temperatures. Mean daily water temperatures ranged between 13.8°C and 21.9°C during days when eggs were collected at San Marcial in 2016.

Rio Grande Silvery Minnow mixture-model estimates ($E(x)$), using standardized egg passage rate data (E_p) from 2003–2016, revealed notable differences across sampling years (Figure 3). Standardized egg passage rates were highest in 2011 (5.40×10^{1}) and lowest in 2004 (9.62×10^{-4}). There was a steady decline from 2011–2013, followed by an increase in 2014. Egg passage rates declined ($P < 0.05$) from 2015 (7.05×10^{-1}) to 2016 (4.91×10^{-2}). Simple estimates of mean egg passage rates, using the method of moments, were similar to mixture-model estimates.

General linear models of Rio Grande Silvery Minnow mixture-model estimates revealed that variation in the mean of the lognormal distribution of E_p (μ) and the probability of occurrence (δ) was reasonably predicted by changes in hydraulic variables (allowing for random effects) over time (2003–2016). The top model (δ(Year) μ(SANmax+R)) received about 37% of the AIC_c weight (w_i) and had an AIC_c value of 1,053.84 (Table 2). The next two models, which accounted for about 42% of the cumulative w_i, were related to the interaction among δ, μ, and hydraulic variables representing persistently low flows (e.g., SAN<100 and SAN<200). The global model (δ(Year) μ(Year)) received only 6% of w_i, and nearly all remaining model combinations (197 out of 200) each received < 1% of w_i. High peak flows were associated with decreased egg passage rates, while extended low flows were associated with increased egg passage rates.

Logistic regression modeling of Rio Grande Silvery Minnow egg presence-absence data revealed strong associations with the percentage change in mean daily discharge just prior to egg collection (X^2 = 34.79 and $P < 0.001$; Figure 4). Flows used to calculate percent change in discharge (Δ) ranged from < 50 cfs to > 3,000 cfs. The probability of collecting eggs ranged from 0.20 (Δ discharge = -50%) to 0.40 (Δ discharge = 0%) during periods of declining or stable flows, respectively. The probability of collecting eggs was predicted to increase rapidly up to about a 100% increase in mean daily discharge between days just prior to egg collection. The probability of collecting eggs during a 100% increase in flow was 0.83 and during a 200% increase was 0.97.

Spatial Spawning Patterns (2016)

Canal-monitoring sites

Sampling at the canal-sites was conducted during weekdays, excluding holidays, from 2 May through 31 May. The cumulative volume of water sampled was similar at the Belen, Peralta, and Socorro canal-sites (7,141.2 m^3, 5,471.2 m^3, and 6,273.5 m^3). Rio Grande Silvery Minnow eggs were only collected at Peralta (n = 4) during 2016 (Table 3 and Figure 5). The number of eggs estimated to be transported downstream of this site, during an average 30-day period, was 7,154.

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Table 1. Rio Grande Silvery Minnow spawning summary data by year, from 1 May to 10 June, at the San Marcial river-site (NS = not sampled).

Year	Sampling Effort (days)	Eggs Present (days)	Eggs Absent (days)	Occurrence[1] (%)
2003	41	18	23	43.9
2004	41	3	38	7.3
2005	NS	NS	NS	NS
2006	41	10	31	24.4
2007	41	39	2	95.1
2008	41	3	38	7.3
2009	41	9	32	22.0
2010	38	15	23	39.5
2011	41	36	5	87.8
2012	41	18	23	43.9
2013	41	13	28	31.7
2014	41	24	17	58.5
2015	39	30	9	76.9
2016	41	13	28	31.7

[1] = Annual occurrence values were the percentage of days when eggs were present, based on the total sampling days.

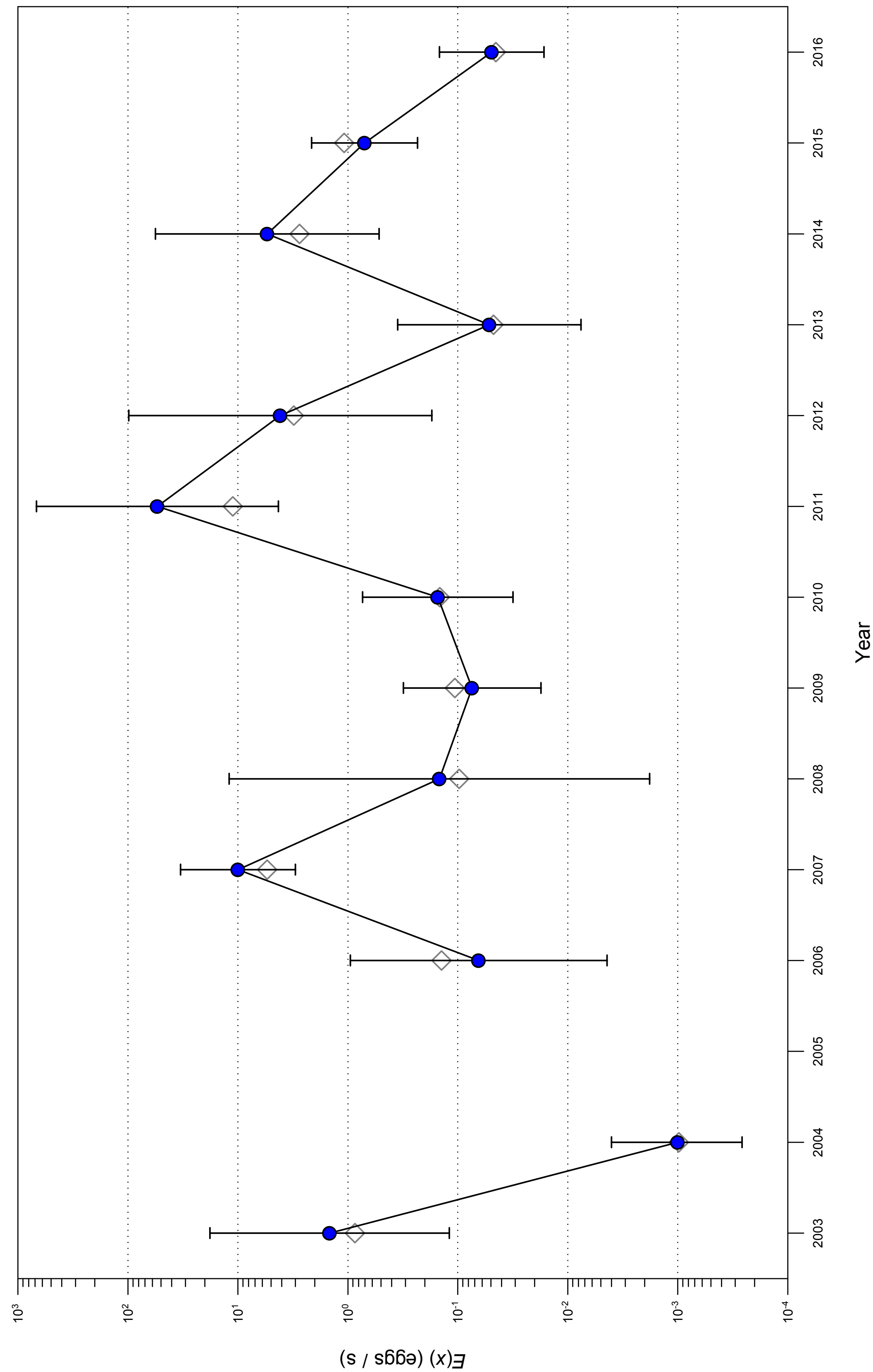

Figure 3. Rio Grande Silvery Minnow mixture-model estimates ($E(x)$) of egg passage rates at the San Marcial river-site, from 1 May to 10 June, across years. Modeled estimates (circles), 95% confidence intervals (bars), and simple estimates using the method of moments (diamonds) are illustrated.

Table 2. General linear models of Rio Grande Silvery Minnow mixture-model estimates using egg passage rate data, from 1 May to 10 June, at the San Marcial river-site (2003–2016).

Model[1]	**logLike**[2]	**K**[3]	**AIC_c**[4]	**w_i**[5]
δ(Year) μ(SANmax+*R*)	1,020.58	16	1,053.84	0.3658
δ(Year) μ(SAN<200+*R*)	1,020.96	16	1,054.23	0.3018
δ(Year) μ(SAN<100+*R*)	1,022.90	16	1,056.16	0.1146
δ(Year) μ(SAN>500+*R*)	1,024.04	16	1,057.31	0.0647
δ(Year) μ(Year)	985.88	33	1,057.32	0.0642
δ(Year) μ(SANmean+*R*)	1,025.35	16	1,058.62	0.0336
δ(Year) μ(SAN>1,500+*R*)	1,026.72	16	1,059.99	0.0169
δ(SAN>2,500+*R*) μ(SAN<200+*R*)	1,041.70	9	1,060.12	0.0159
δ(SAN>2,500+*R*) μ(SAN<100+*R*)	1,043.86	9	1,062.27	0.0054
δ(SANmean+*R*) μ(SAN<200+*R*)	1,044.14	9	1,062.55	0.0047

[1] = Model variables included year (2003–2004, 2007–2012, 2014–2016) and hydraulic variables at USGS Gage #08358400 (SAN; Rio Grande Floodway at San Marcial, NM), allowing for random effects (*R*).

[2] = Models included -2[log-likelihood] values.

[3] = Models had different numbers of parameters (K), depending on their complexity.

[4] = Models were ranked by Akaike’s information criterion values (AIC_c).

[5] = Models included AIC_c weights (w_i).

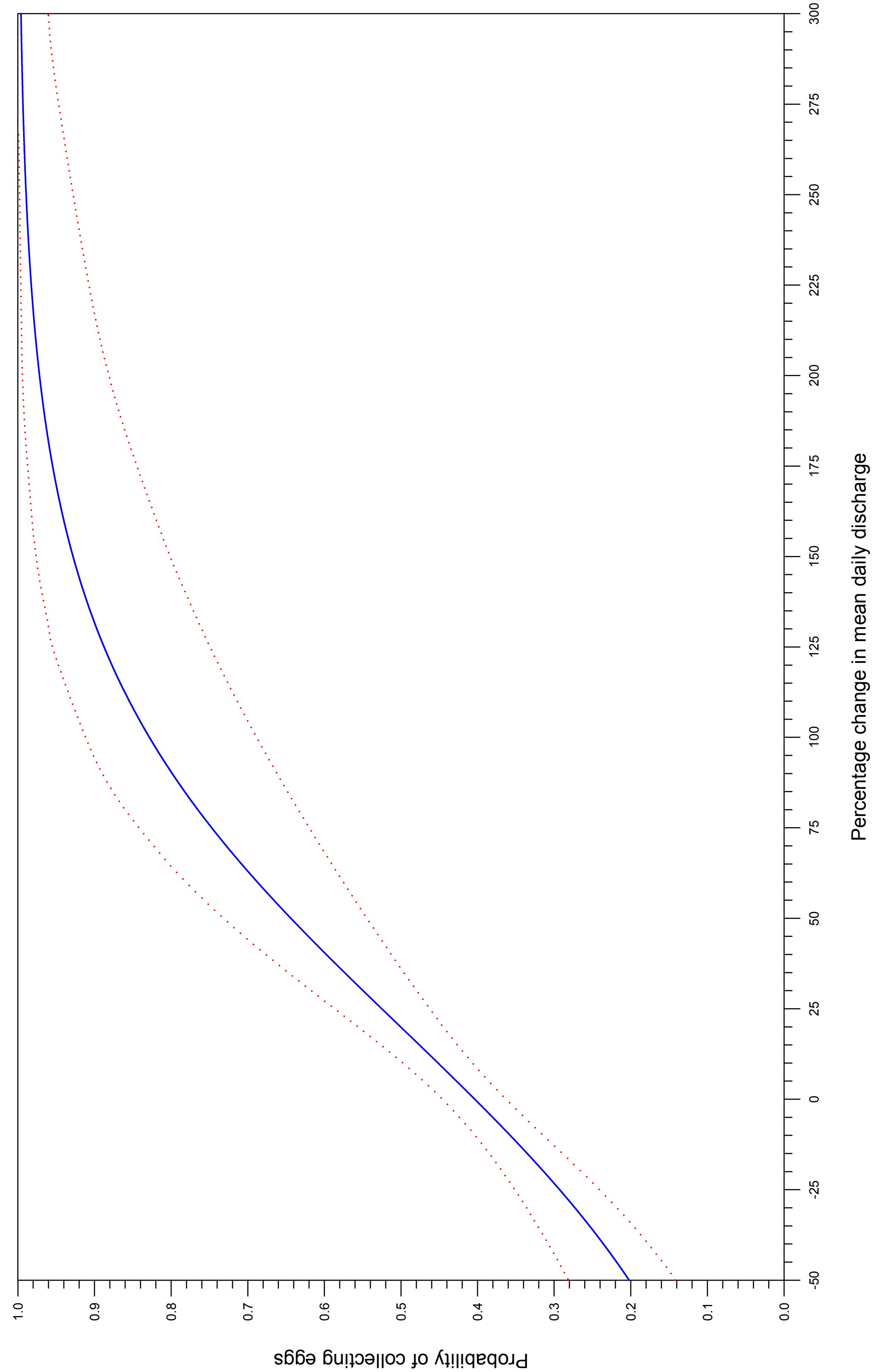

Figure 4. Logistic regression plot, using San Marcial river-site data from 1 May to 10 June (2003–2016), illustrating the probability of collecting eggs as a function of the percentage change in mean daily discharge from two days to one day prior to egg collection. Graph shows logistic regression line (solid) and 95% confidence intervals (dotted).

Table 3. Number of Rio Grande Silvery Minnow eggs collected per day at each of the six sampling localities.

Sampling Date[1]	**Belen Canal-Site**	**Peralta Canal-Site**	**Socorro Canal-Site**	**Isleta River-Site**	**San Acacia River-Site**	**San Marcial River-Site**
23-Apr-16	NS	NS	NS	NS	NS	24
24-Apr-16	NS	NS	NS	NS	NS	43
25-Apr-16	NS	NS	NS	NS	NS	43
26-Apr-16	NS	NS	NS	NS	NS	172
27-Apr-16	NS	NS	NS	NS	NS	11
29-Apr-16	NS	NS	NS	NS	NS	1
30-Apr-16	NS	NS	NS	NS	NS	12
1-May-16	NS	NS	NS	NS	NS	2
2-May-16	0	0	0	0	1	0
6-May-16	0	3	0	1	3	3
7-May-16	NS	NS	NS	NS	NS	1
12-May-16	0	1	0	0	0	0
13-May-16	0	0	0	0	4	0
14-May-16	NS	NS	NS	NS	NS	67
15-May-16	NS	NS	NS	NS	NS	75
16-May-16	0	0	0	2	0	2
17-May-16	0	0	0	0	0	1
19-May-16	0	0	0	0	0	2
20-May-16	0	0	0	0	2	14
21-May-16	NS	NS	NS	NS	NS	1
23-May-16	0	0	0	1	0	2
24-May-16	0	0	0	1	0	4
25-May-16	0	0	0	0	0	1
TOTAL (EGGS)	0	4	0	5	10	481

[1] = Table does not include dates that eggs were not collected at any of the sampling localities (NS = Not Sampled; only San Marcial river-site sampled on weekends/holidays).

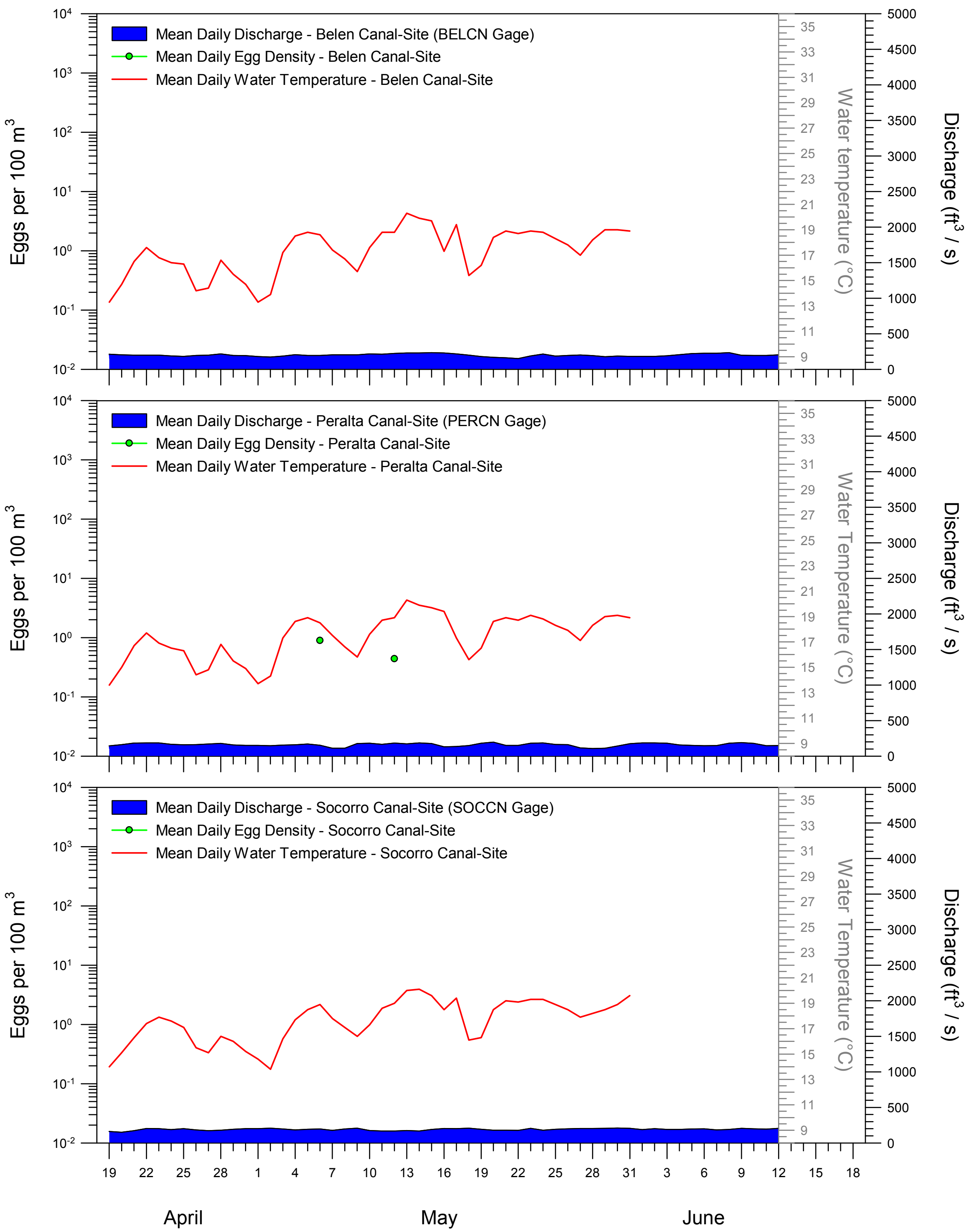

Figure 5. Mean daily discharge, egg density (May), and water temperature during the 2016 Rio Grande Silvery Minnow spawning periodicity study at the canal-monitoring sites.

River-monitoring sites

Sampling at the Isleta and San Acacia river-sites was conducted during weekdays, excluding holidays, from 2 May through 31 May. Sampling at the San Marcial river-site was conducted daily from 22 April through 10 June. The cumulative volume of water sampled at Isleta and San Acacia was similar (4,311.1 m^3 and 4,417.5 m^3, respectively) but notably higher at San Marcial (70,690.9 m^3). Sampling at San Marcial occurred over a longer duration (i.e., more days and hours/day) as compared with the two upstream river-sites. Rio Grande Silvery Minnow spawning was documented at all three sites (see Table 3). The three sites yielded 496 eggs; the vast majority was collected at San Marcial (n = 481; Figure 6). The number of eggs estimated to be transported downstream, during an average 30-day period, was 166,147 at Isleta, 144,374 at San Acacia, and 127,267 at San Marcial.

Comparisons among canal and river monitoring sites

The mixture-model was used to estimate and compare longitudinal egg passage rates in 2016 at the Isleta (0.06), San Acacia (0.06), and San Marcial (0.07) river-sites (Figure 7). However, there were no differences ($P > 0.05$) between the Isleta, San Acacia, and San Marcial estimates. All three sites had a decline in egg passage rates from 2015 to 2016; the decline was significant ($P < 0.05$) at San Marcial.

Sampling at the Belen and Peralta canal-sites was longitudinally comparable to sampling at the Isleta river-site. Water temperatures during May were similar among these three sampling sites (range ≈ 13°C to 20°C), and differences in temperatures were typically < 0.5°C. There were four eggs collected at the Peralta canal-site, none at the Belen canal-site, and five at the Isleta river-site. The estimated egg passage rate at the Isleta river-site (0.06) was higher ($P < 0.05$) than at the Belen (0.0) or Peralta canal-sites (0.003). The estimated proportion of eggs entrained into the canals was 0.05.

From 19 April to 12 June, flows at the Belen canal-site ranged from 152 to 235 cfs (mean = 200.6 cfs). Flows at the Peralta canal-site were slightly lower and ranged from 106 to 196 cfs (mean = 160.2 cfs). In contrast, flows at the Isleta river-site during the same period were higher and more variable (range = 767 to 3,570 cfs; mean = 1,815.2 cfs) as compared with either of the two canal-sites. The estimated proportion of river water diverted into the canals at this longitudinal location was 0.17.

Sampling at the Socorro canal-site was longitudinally comparable to sampling at the San Acacia river-site. Water temperatures during May were similar between these two sites (range ≈ 14°C to 21°C); the difference in mean daily temperatures was generally < 0.5°C. While eggs were not collected at the Socorro canal-site, we collected 10 eggs at the San Acacia river-site. The estimated egg passage rate at the San Acacia river-site (0.06) was higher ($P < 0.05$) than at the Socorro canal-site (0.0), and the estimated proportion of eggs entrained into the canal was 0.0.

From 19 April to 12 June, flows at the Socorro canal-site ranged from 151 to 210 cfs (mean = 190.5 cfs). Water at the Socorro canal-site originated only from sources upstream of San Acacia Diversion Dam (e.g., Isleta Diversion Dam). Flows at the San Acacia river-site were higher and more variable (range = 352 to 2,700 cfs; mean = 1,325.2 cfs) as compared with the Socorro canal-site. The estimated proportion of river water diverted into the canal at San Acacia Diversion Dam was 0.0, and the estimated proportion of water in the canal (as compared with the river at this longitudinal location) was 0.13.

The estimated densities of eggs were also compared across canal and river monitoring sites in both the Isleta and San Acacia reaches. In the Isleta Reach, the estimated egg density was highest at the Isleta river-site (0.13), followed by the Peralta (0.06) and Belen (0.0) canal-sites. However, the estimated egg density at the Isleta river-site was not different ($P > 0.05$) from the estimated egg density at either the Peralta canal-site or at the two canal-sites combined (0.03). In the San Acacia Reach, the estimated egg density at the San Acacia river-site (0.23) was higher ($P < 0.05$) than at the Socorro canal-site (0.0).

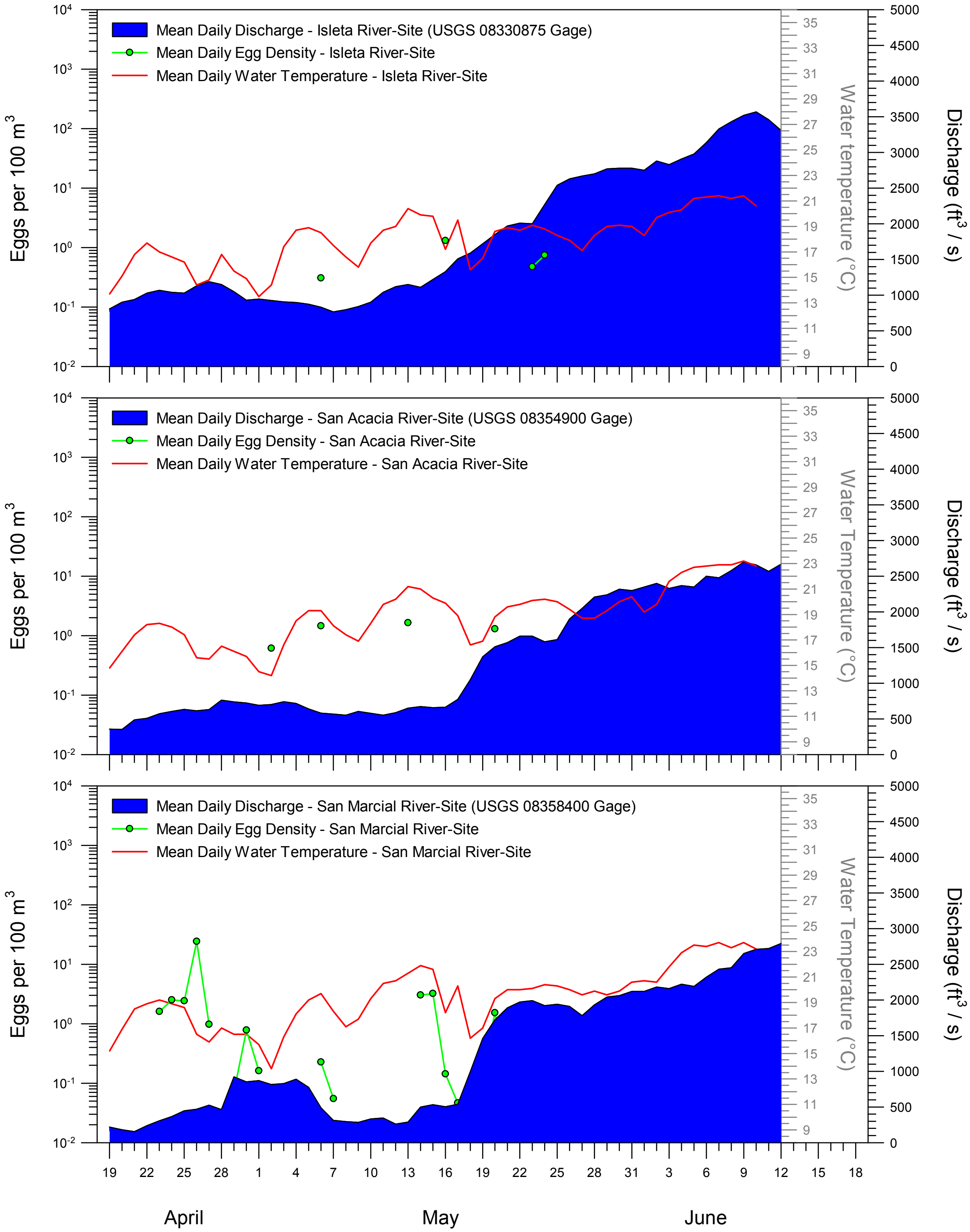

Figure 6. Mean daily discharge, egg density (Isleta and San Acacia [May]; San Marcial [22 April to 10 June]), and mean daily water temperature during the 2016 Rio Grande Silvery Minnow spawning periodicity study at the river-monitoring sites.

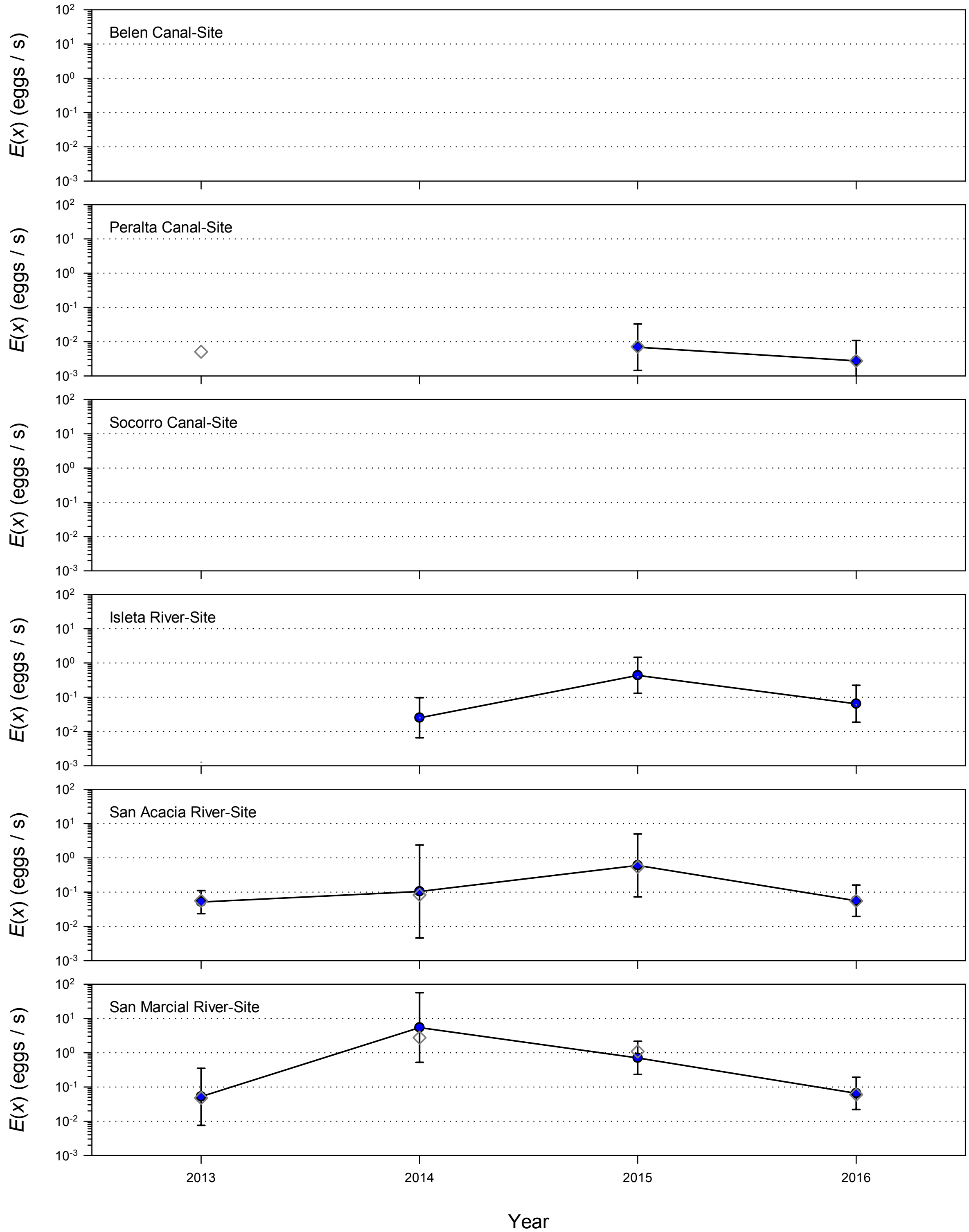

Figure 7. Rio Grande Silvery Minnow mixture-model estimates ($E(x)$) of egg passage rates, during May, across sites and years. Modeled estimates (circles), 95% confidence intervals (bars), and simple estimates using the method of moments (diamonds) are illustrated.

DISCUSSION

The negative impacts of dam-related modifications on the native fishes of the Great Plains have been well documented (Stanford and Ward, 1979; Cross et al., 1983; Cross et al. 1985, Cross and Moss, 1987; Winston et al., 1991; Luttrell et al., 1999). The extensive fragmentation and channelization of rivers in the American Southwest have specifically led to the decline or extirpation of many pelagic spawning cyprinids, whose reproductive propagules drift downstream of instream barriers or into unsuitable reservoir habitats (Dudley and Platania, 2007). In the Middle Rio Grande, large numbers of Rio Grande Silvery Minnow eggs are displaced downstream every year during spawning season (Dudley and Platania, 2015). The downstream transport of eggs and larvae likely contributed to the loss of this species from the Cochiti Reach and to its decline in the Angostura Reach (Platania and Altenbach, 1998).

In addition to the problems created by river fragmentation, habitat simplification (caused by flow regulation, bank armoring, etc.) also appears to contribute to the downstream displacement of Rio Grande Silvery Minnow eggs. The closure of Cochiti Dam resulted in a greatly reduced passage of fine sediments that has, in turn, contributed to channel degradation, armoring, and narrowing (Lagasse, 1985). While arroyos, backwaters, and other “nursery habitats” may result in increased upstream retention of eggs (Porter and Massong, 2004a; Porter and Massong, 2004b; Pease et al., 2006), these low velocity mesohabitats are relatively rare, particularly in incised portions of the river.

Spawning by Rio Grande Silvery Minnow, and other members of its reproductive guild, is triggered by specific environmental cues (Platania and Altenbach, 1998). These fishes typically spawn shortly after increases in flow during the spring and summer. Elevated flows result in increased water velocities/depths in some areas and inundated habitats in other areas. Additionally, there are frequently changes in water chemistry that accompany flow increases, particularly when large amounts of sediment are carried into the river from formerly dry shoreline areas, eroding banks, or flowing arroyos. The increased sediment load results in increased turbidity levels (decreased water clarity), slightly decreased water temperatures, and can lead to substantial increases in salinity levels. It is likely that Rio Grande Silvery Minnow are spawning as a result of some combination of these altered habitat and water chemistry conditions during increased flow events.

While increases in discharge appear to be the primary cue for spawning, water temperature seems to be an important factor as well. Spawning occurs over a relatively wide range of mean daily water temperatures (ca. 13 to 26°C), but the majority occurs over a much narrower range (ca. 17 to 23°C). This interaction, however, is complex and varies among years and reaches. Spawning has been documented from late March into late June (Platania and Dudley, 2000). The mean daily water temperatures during these extended periods were at the limits of the range at which spawning has been documented. Prior to spawning, the gonadosomatic index (GSI) values of Rio Grande Silvery Minnow increase during early spring (Platania and Altenbach, 1996). The GSI value is the ratio of gonad weight to body weight, and higher GSI values indicate an increased physiological, and perhaps behavioral, readiness to spawn. Field collections (1993–1995) indicated that elevated GSI values corresponded with the increased water temperatures of spring (Platania and Altenbach, 1996).

It is possible that the typical range of spawning temperatures is even broader, particularly at warmer water temperatures, but there have been no longer-duration systematic studies conducted to document this possibility. Despite the lack of field spawning studies earlier or later in the year, experimental water temperature treatments on eggs and larvae of Rio Grande Silvery Minnow revealed that mortality was notably higher at 15°C or 30°C as compared with 20°C or 25°C (Platania, 2000). It is likely that individuals spawned earlier in the year (e.g., March) or later in the year (e.g., July), when water temperatures are at the presumed limits of their spawning range, have an increased rate of mortality. However, individuals spawned slightly earlier in the year might have an increased chance of survival as compared to those spawned later in the year, since there would presumably be reduced competitive pressure from other larval fishes for food resources (Pease et al., 2006), which become widely available shortly after the seasonal inundation of floodplain habitats (Junk et al., 1989).

At the San Marcial river-site, Rio Grande Silvery Minnow spawned relatively earlier in 2016 (late April) than in most years (mid-May). Flows were relatively low during mid-April of 2016, but then rose (along with water temperatures) during the latter part of the month. Similar spawning periodicity patterns have also been noted in past sampling years (e.g., 2009 and 2011). It is likely that the synergistic combination of rising water temperatures and flows created an earlier spring spawning stimulus in these years. While earlier spawning could be beneficial to this species, their survival ultimately depends on many factors.

The recruitment of Rio Grande Silvery Minnow, through the spring and summer, is likely affected by both abiotic (e.g., flow, temperature, water quality) and biotic (e.g., temporal/spatial food availability, competitive interactions, predation pressure) factors. Genetic analyses of wild eggs and adults suggest that survival is highly variable, leading to large differences in reproductive success among individuals (Osborne et al., 2005). Additionally, it is unknown if reproductive success varies among individuals according to the spawning strategy employed within a single season (i.e., single spawning vs. multiple spawning). In fact, the broad range of conditions that result in Rio Grande Silvery Minnow reproduction could indicate that there is no ideal spawning cue (i.e., combination of abiotic/biotic conditions) that would result in a consistently higher chance of early survival and recruitment. The closest combination of favorable conditions, based on the last decade of spawning studies, appears to be increased flows that occur with appropriately warm water temperatures.

While increased flows can lead to expanded larval fish nursery habitats and presumably higher recruitment success, there is no guarantee that flows will continue to rise or be sustained after spawning. Flows will sometimes briefly increase and then return to low levels either as a result of changes in ambient temperature (affecting the rate of snowmelt) or as a result of short-term precipitation events. The young that are produced as a result of these flow events are subjected to biotic and physical conditions that may preclude their successful growth and survivorship, particularly during summer months. Excessively elevated water temperatures (> 30°C) in the Rio Grande, caused by warm ambient conditions and low flows, may reduce the hatching success of eggs and survival of larvae (Platania, 2000). In addition to high water temperatures and possibly poor water quality, the likelihood of negative biotic interactions (e.g., predation or competition) would likely increase as suitable habitats contract during low flows.

The top general linear models, based on the long-term spawning data (2003–2016), indicated that high peak flows were associated with decreased egg passage rates, while extended low flows were associated with increased egg passage rates. The physical conditions produced by prolonged and elevated flows during spring result in overbank flooding of vegetated areas, formation of inundated habitats within the river channel, and creation of shoreline and island backwaters. Shallow low-velocity habitats (e.g., shoreline pools, backwaters, overbank floodplains etc.) are well known to be essential for the retention and successful recruitment of early life history stages of many freshwater fish species throughout the world (for review see Welcomme, 1979). Similar processes are likely important for the successful survival and recruitment of the Middle Rio Grande ichthyofaunal community, including early life stages of Rio Grande Silvery Minnow (Pease et al., 2006; Turner et al., 2010). It is likely that higher numbers of eggs are retained upstream during years with sustained high flow events, which would account for their reduced displacement past our sampling site. In contrast, short-duration and low magnitude flow events, which typically occurred during years with extended low flows, appeared to result in the elevated downstream transport of eggs. Differences between downstream egg passage rates during high and low flow years, and their presumed effects on survival and recruitment, could help explain the increased autumnal density of Rio Grande Silvery Minnow during years with elevated and sustained flows during spring (Dudley et al., 2016).

Efforts were made to estimate the number of eggs transported downstream of each sampling site based on the number of eggs collected, volume of water sampled, mean daily discharge, and duration of sampling. This approach required several simplifying assumptions including: 1) eggs were approximately evenly distributed within the volume of water passing the sampling site, 2) eggs collected during a given day approximately represented the rate at which eggs were transported downstream of the site during that day, and 3) the discharge at the nearest upstream USGS station approximately represented the discharge at the sampling site. While these assumptions seem reasonable, some non-quantified error was likely introduced into the calculations through these extrapolations. For example, the use of multiple MECs may more accurately characterize spatial differences in the densities of drifting fish eggs across the river channel (Worthington et al., 2013a; b). However, the number of eggs estimated to be transported downstream during spawning events would still be quite high even with modest violations of these assumptions. These results indicate a substantial downstream transport of drifting eggs at the San

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Marcial river-site despite the seemingly modest numbers of eggs collected in individual MECs. It is unknown, however, what proportion of these eggs was viable since that was not a study objective.

The total number of Rio Grande Silvery Minnow eggs collected was generally obtained through direct counting of individual propagules in the field. This direct counting method was used for nearly all sampling days during the spawning season across years. However, there was an occasional need to preserve egg samples when the total number of eggs collected exceeded our ability to accurately count them while also effectively operating the MECs. This threshold was exceeded when more than about 1,000 eggs were collected every hour. While these elevated spawning events have occurred only a few times since this study began, the need to accurately quantify the number of eggs was particularly crucial since these events compose the vast majority of the total spawning effort within a given year. Since 2002, we have only used actual eggs counts because we found that volumetric determination lacked the adequate rigor necessary to obtain an accurate count. Based on several trials conducted in 2011, we also determined that time-based estimates of the number of eggs collected were even more problematic than volumetric estimates, consistently resulting in inaccurate egg counts (Dudley and Platania, 2011).

Since Rio Grande Silvery Minnow is the only extant species of the reproductive guild of pelagic spawning cyprinids in the Middle Rio Grande, the species-specific identification of any semibuoyant egg collected during this study was unambiguous. The only other fish eggs that we have captured during this and previous investigations were those of the Common Carp, *Cyprinus carpio*. Fortunately, there are numerous differences between eggs of these species that aid in identification. As the eggs of Common Carp are adhesive, there are usually small pieces of particulate matter attached to the chorion. Additionally, Common Carp eggs are smaller and more opaque than Rio Grande Silvery Minnow eggs, and the eyes of carp embryos become pigmented very early in development. Conversely, the minnow eggs are clear, non-adhesive, smooth, large, and the embryos lack discernible pigment.

The total number of Rio Grande Silvery Minnow eggs collected at a site, from multiple MECs within a day, was combined for the purposes of this report. The variation in egg densities among MECs and different sequential periods in a day was minimal compared to the variation across days. The primary purpose in sampling with two MECs over an extended duration at the San Marcial river-site was to both detect the presence of eggs and to obtain an accurate estimate of the egg passage rate over time.

Our long-term spawning study results indicate that substantial numbers of Rio Grande Silvery Minnow eggs, and presumably larvae, are being transported downstream every year. Additionally, the highest egg passage rates generally occur in the San Acacia Reach. In support of these observations, the highest densities of juvenile Rio Grande Silvery Minnow are most frequently found in the southern reaches of the Middle Rio Grande following annual spawning (Dudley et al., 2016). This trend was first noted over two decades ago (Bestgen and Platania, 1991), before Rio Grande Silvery Minnow was listed as a federally endangered species, and it persists to the present time. The few exceptions to this trend (i.e., higher densities of juveniles found in upstream reaches) have almost always occurred during years when flows were exceptionally low in the San Acacia Reach, resulting in substantial drying and loss of fish in those areas.

Despite the seemingly large number of Rio Grande Silvery Minnow propagules transported downstream every year, some portion remains upstream (Dudley and Platania, 2007; Widmer et al., 2012). It is likely that the proportion of individuals retained and successfully recruited upstream is related to the complexity of instream habitat conditions and the long-term availability of nursery habitat. The availability of floodplain habitat could be particularly important, as these areas are likely locations for the reduced transport rate and increased retention of drifting fish eggs (Dudley and Platania, 2007; Widmer et al., 2012; Gonzales et al., 2014). Since successful growth and survival of Rio Grande Silvery Minnow from the egg through the early larval stages requires at least three weeks (Platania, 1995), the persistence of these nursery habitats is essential during this critical phase of development.

Sampling from multiple canal and river locations in the Isleta and San Acacia reaches since 2013 provided additional insight to spatial spawning patterns. The egg passage rate at the San Marcial river-site in 2016 indicated a marked decrease in the number of eggs displaced downstream as compared with 2015. While low numbers of eggs in 2016 precluded robust comparisons of spatial spawning patterns among canal-monitoring sites, it was apparent from the river-monitoring data that egg passage rates were similar in the Isleta and San Acacia reaches. Although flows were notably lower at the canal-monitoring sites as compared with the river-monitoring sites, there were no appreciable differences in water temperature between canal and river sites.

There were, however, differences in the estimated egg passage rates between the Socorro canal-site and the San Acacia river-site, which appear to be driven by the source of the canal water. Specifically, the absence of water being diverted at San Acacia Diversion Dam during river spawning events apparently helped to minimize the entrainment of eggs into the San Acacia Reach irrigation network (e.g., Socorro canal-site) during 2016. This managed timing of water diversions (i.e., to avoid peak spawning events) is an important conservation measure to help minimize the numbers of both drifting eggs and larvae that would otherwise be entrained into unsuitable areas.

In contrast, there was no apparent managed timing of water diversions (i.e., to avoid peak spawning events) in the Isleta Reach during 2016. While a relatively lower proportion of eggs were entrained into the canals as compared to the estimated proportion of water diverted, those results were based on sparse data ($n < 10$ eggs). Further, the estimated densities of eggs didn't differ between the Isleta river-site and the two canal-sites combined, even though no eggs were collected in the Belen canal-site. It seems more reasonable that the slight differences in egg densities and entrainment estimates across the Isleta Reach sites were caused by chance sampling events, which were accentuated because of the low numbers of eggs collected in 2016.

While Rio Grande Silvery Minnow has declined markedly throughout its range since 2009, the improved spring runoffs of 2015 and 2016 resulted in decreased egg passage rates as compared with 2014. However, the recruitment success of this species during the fall of 2016 will likely be highly dependent on summer flow conditions. The loss of individuals from downstream reaches during river drying events is particularly pertinent, as the occurrence and density of this species is consistently higher in these vulnerable areas (Dudley et al., 2016). The future conservation status of Rio Grande Silvery Minnow appears strongly dependent on reliably ensuring appropriate seasonal flow and habitat conditions to support the crucial spawning and early recruitment phases of this species.

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