Drift and Retention of Pelagic Spawning Minnow Eggs in a Regulated River

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ABSTRACT

Long-distance drift of eggs and larvae has been identified as a possible cause of downstream displacement and poor recruitment of the endangered Rio Grande silvery minnow (*Hybognathus amarus*; silvery minnow). Seven experiments were conducted using artificial eggs to estimate silvery minnow egg drift and retention in the Albuquerque and Isleta reaches of the regulated Middle Rio Grande, New Mexico, USA over a range of flows during expected spawning times. Bead retention varied by reach, discharge, and shape of the hydrograph. Highest retention (6.9% and 9.7% per km in the Albuquerque and Isleta reaches, respectively) occurred on the ascending limb of a high flow in areas where there was substantial floodplain inundation. Retention was maximized at different flows in each reach (97 and 140 m^3/s, respectively), possibly associated with reach-specific floodplain inundation thresholds. Lowest retention in each reach (2.1% and 1.7%, respectively) occurred on the descending limb of low and high flows, respectively. Of the silvery minnow eggs produced in the combined Albuquerque and Isleta reaches in 2005, 8–14% are predicted to have been retained in the Albuquerque Reach (67 km) and 49–83% in the Isleta Reach (86 km) based on the distribution of adult fish and measured bead retention rates. Although silvery minnow propagules are capable of drifting long distances, our study suggests that considerable retention occurs in the Middle Rio Grande. Habitat restoration to increase channel habitat complexity, and flow management to promote floodplain inundation should help to retain a greater proportion of propagules in upstream reaches.

KEY WORDS: Rio Grande silvery minnow, *Hybognathus amarus*, egg drift, gellan gum beads, Middle Rio Grande, pelagic spawning, egg retention, habitat restoration

INTRODUCTION

Egg and larval fish dispersal by passive downstream drift is characteristic of many riverine fish species (e.g., Muth and Schumulbach, 1984; Tyus, 1990; Robinson *et al.*, 1998; Medley *et al.*, 2007; Dudley and Platania, 2007). Downstream transport of these propagules must be countered by an upstream movement of subsequent life stages for a population to maintain its longitudinal position in the river (Brown and Armstrong, 1985). Large-bodied fishes may migrate long distances upstream to counter displacement (Tyus, 1990; Osmundson *et al.*, 1998; Humphries and Lake, 2000). Extensive migrations of short-lived, small-bodied fishes are undocumented, although some species are physically capable of swimming long distances (Bestgen *et al.* 2010). Downstream transport of some individuals is important in expanding populations and for maintaining genetic diversity (Alò and Turner, 2005), particularly in areas of high spatial and temporal environmental variability. However, it is hypothesized that small-bodied riverine fishes have evolved reproductive strategies involving the timing and location of egg release to retain a large proportion of their offspring close to population centers (Medley *et al.*, 2007). Reproductive strategies that minimize long-distance movements allow the population to allocate a greater proportion of its energy reserves to growth and reproduction (Evans and Claiborne, 2005).

During periods of increasing or high flows, such as those caused by snowmelt, summer rainstorms, or reservoir releases, several small-bodied cyprinid species of the Rio Grande Basin spawn by releasing semi-buoyant, non-adhesive eggs that may be transported downstream by river currents (Platania and Altenbach, 1998). Eggs and larvae drift passively with the current until the larvae develop air bladders and actively seek low-velocity nursery habitats 3–5 d post-spawning (Platania, 1995; Platania and Altenbach, 1998). The distance that propagules are transported is hypothesized to be influenced by channel shape and complexity, hydrograph magnitude and shape, and river floodplain connectivity (Porter and Massong, 2006; Dudley and Platania, 2007; Medley *et al.*, 2007). Broad, complex channel reaches with a large interaction between the channel bed and flows slow egg transport velocity (Dudley and Platania, 2007) and eggs are efficiently retained in numerous zero and low-velocity habitats (Porter and Massong, 2006; Medley *et al.*, 2007). Experiments on the Pecos River showed that attenuation of flood flows during the ascending limb of the hydrograph may also retard the downstream transport of eggs, particularly during floodplain inundation as eggs are stored concomitant with channel storage (Medley *et al.*, 2007). The loss of habitat diversity and floodplain connection in the Rio Grande Basin associated with river straightening and confinement (Molles *et al.*, 1998; Cowley, 2006; Pease *et al.*, 2006) is believed to have increased the transport distances of pelagic eggs, which may have contributed to the local decline of native pelagic-spawning cyprinid populations (Dudley and Platania, 2007).

The endangered Rio Grande silvery minnow (*Hybognathus amarus*; silvery minnow) is the only remaining pelagic-spawning cyprinid in the Middle Rio Grande of New Mexico, USA. The species' range is currently restricted to 275 km between Cochiti Dam and Elephant Butte Reservoir (Bestgen and Platania, 1991). The Middle Rio Grande is divided into four reaches (Cochiti, Albuquerque, Isleta, and San Acacia) by three irrigation diversion dams (Angostura, Isleta, and San Acacia; Figure 1). The Albuquerque Reach is bound by the Angostura and Isleta diversion dams and the Isleta Reach is bound by the Isleta and San Acacia diversion dams. Flow through the Middle Rio Grande is largely regulated by Cochiti Dam, which was built in 1973 for flood and sediment control, with periodic inflows from unregulated tributaries. The three irrigation diversion dams seasonally divert a proportion of the flow for agricultural use; these dams permit the downstream passage of silvery minnow propagules and restrict upstream movement of juveniles and adults.

The silvery minnow spawns in late spring and early summer (May to June) in association with spring runoff and at water temperatures of 16-27°C (Platania, 1995). It is believed that the species spawns in river currents that transport propagules downstream (Platania and Altenbach, 1998) or it may spawn on inundated floodplains (Pease *et al.*, 2006). Historical transport distances of silvery minnow eggs are unknown, but long-distance downstream drift of propagules has been implicated in downstream displacement of the population and poor recruitment in the contemporary Middle Rio Grande (Dudley and Platania, 2001; Dudley and Platania, 2002; Dudley and Platania, 2007). It is estimated that eggs can be transported up to 216–359 km downstream during 3–5 d of passive drift, depending on river flows (U.S. Fish and Wildlife Service [USFWS], 2003). Bestgen *et al.* (2010) conducted laboratory tests that routinely documented silvery minnow swimming 50 km in <72 h in water moving 60 cm/s, so this species may be capable of performing long upstream migrations to counteract downstream transport of eggs. However, the physiological cost of migrating >100 km is unknown and it is poorly understood whether silvery minnow exhibit migratory behavior in the wild.

Dudley and Platania (2007) modeled transport of silvery minnow propagules in the Middle Rio Grande and concluded that reaches less than 100 km in length cannot support long-term self-sustaining populations. They proposed a long-term management strategy of removing diversion dams, starting with those that are obsolete or whose primary purpose is to divert water for irrigation, and restoring natural flow regimes in the Rio Grande. We hypothesize that shorter reaches of river (<100 km) can maintain self-sustaining silvery minnow populations in the Middle Rio Grande provided complex habitats for retention and recruitment and suitable flow conditions are available. Medley *et al.* (2007) found that broad, complex reaches of the Pecos River (sand-bed river similar to the Middle Rio Grande) retained up to 90% of artificial eggs within 50 km of their release point during hydrologic conditions that stimulated spawning (i.e., the ascending limb of a flood pulse). They concluded that habitat restoration to reverse the loss of channel complexity and floodplain connectivity is likely to be a beneficial conservation strategy (Medley *et al.*, 2007). This relatively short drift distance would preclude the need for long, upstream migrations in order to maintain core populations.

We conducted a series of experiments where artificial eggs were released at different flows in the Albuquerque and Isleta reaches of the Middle Rio Grande. Egg and larval retention in these reaches was previously assumed to be poor, contributing to low recruitment and the concentration of silvery minnow in the San Acacia Reach (USFWS, 2003). The range of flows tested represented a large proportion of the range of snowmelt runoff flows that occur in this regulated stretch of river. Experiments were conducted on both the rising and falling limbs of the spring hydrograph. The specific goals of the study were to document egg drift and retention rates and to test the previously hypothesized role of flood attenuation and channel storage to promote egg retention. Information from these studies will be used to identify reaches with the highest retention of propagules, help to direct habitat restoration, and guide flow management of the Middle Rio Grande.

METHODS

Experimental Design

Seven experiments were conducted in 2005 and 2007 to quantify the retention of artificial eggs (gellan gum beads; Key Essentials, Inc., Rancho Santa Margarita, California, USA) in the Albuquerque and Isleta reaches of the Middle Rio Grande over nearly the full range of reservoir releases during snowmelt runoff. Flows ranged from 17 to 147 m^3/s at the U.S. Geological Survey (USGS) Albuquerque gage (Figure 2). Experiments 1, 1a, and 4 were conducted during the ascending limb of the high spring flow and immediately after a flood pulse release from Cochiti Dam; these conditions stimulate silvery minnow to spawn (Platania and Altenbach, 1998). Experiments 2 and 5 were conducted during the descending limb of the high spring flow, and experiments 3 and 6 occurred during periods of relatively low flow. Substantial floodplain inundation occurred in the Isleta Reach during the ascending limb experiment in 2005 (experiments 1, 1a), but did not occur in the five other experiments. The two lower-flow experiments (3 and 6) occurred towards the end of the snowmelt period at river discharges exceeding base flow. Mean flows during the experiments were compared to mean May flows for the period of record (1974-2009) at the Rio Grande at Albuquerque Gage (USGS 08330000). Flows during experiments 1 and 1a were in the 88 percentile of mean May flows, experiment 2 in the 81 percentile, experiment 3 in the 29 percentile, experiment 4 in the 55 percentile, experiment 5 in the 43 percentile, and experiment 6 in the 17 percentile.

Beads were released into the thalweg below Angostura Diversion Dam for experiments 1, 3, 4, 5, and 6 and into the thalweg below Isleta Diversion Dam for experiments 1a and 2 (Figure 1, Table 1). Different colors of beads were released below the two diversion dams in experiment 1 and 1a. For experiments 1, 1a, and 4 on the ascending limb of the hydrograph, beads were released within 1 h of the flood pulse passing the release site. Beads were collected near the mouth of the South Diversion Channel (SDC) except during experiments 1a and 2, and at San Acacia except during experiments 3 and 6.

Beads were collected using Moore Egg Collectors (MECs) (Altenbach *et al.*, 2000) for 48 h after the initial arrival of beads, or until bead collection rates were low and stable for several hours. Sampling occurred in water 0.6–1.2 m deep, regardless of river discharge. Beads were collected in 15-min intervals and counted in the field. In 2005, samples were collected from two alternating MECs. In 2007, two to four MECs were operated concurrently and the catch rate was averaged for each 15-min period. Water velocity through the MEC was measured continuously with a flow meter (General Oceanics, Inc., Miami, Florida, USA) mounted inside each device (2005), or with a 30-second average FloMate portable water velocity meter (Marsh-McBirney, Inc., Loveland, Colorado, USA) held in the MEC intake once at the midpoint of the sample period (2007). The volume of water sampled was calculated from the velocity measurement, time sampled, and area of the MEC intake. The number of beads per volume of water sampled was calculated for each 15-min sample and expanded by river discharge to estimate the number of beads passing a given collection site in each 15-min period.

Durability of Gellan Gum Beads

Gellan gum beads were used as surrogates for silvery minnow eggs (Reinert *et al.*, 2004; Cowley *et al.*, 2005; Medley *et al.*, 2007). Beads were purchased in 208-L drums and prepared by draining packing syrups, rinsing, and soaking in tap water for one week. Once prepared, the beads had the approximate size, shape, and physical properties of silvery minnow eggs (Cowley *et al.*, 2005). The numbers of beads in each drum was estimated from bead counts of 100-mL aliquots.

Gellan beads are organic and naturally break down and disintegrate over time. To determine whether the beads would break down during the span of this experiment, we tested their durability in a series of controlled experiments. Thirty beads were placed in each of 12 1.9-L canning jars filled with turbid Rio Grande water collected from the Central Bridge in Albuquerque during January 2009, and randomly assigned to one of four treatments: 48, 96, or 144 h of continuous mixing, or 144 h in still water, stirred once daily. Three groups of thirty beads were also assigned to a 0 h mixing treatment group; these beads were measured and discarded, without placement in jars. Mixing was produced by aeration through air stones; the beads frequently brushed against the air stones as they circulated in the jars. The numbers of undamaged beads, mean bead diameter, and mean bead weight were measured before and after each treatment. Mean bead diameter was determined by measuring the longest and shortest axis with calipers and by calculating the mean of the two measurements (Reinert *et al.*, 2004). No significant differences in mean bead mass (One-way ANOVA, $F_{4,10} = 0.9333$, $P = 0.48$) or mean bead diameter (One-way ANOVA, $F_{4,10} = 0.9194$, $P = 0.48$) were detected after 0, 48, 96, or 144 h of continuous mixing in river water or 144 h in still river water. We concluded that the beads were suitable for this study, which collected beads up to 5 d (120 h) after release.

Hydrology Modeling

Modeled river flows were used to estimate discharge instead of USGS gage measured flows, because gages were not available at all sites and because some gages in the Middle Rio Grande are inaccurate during snowmelt runoff due to sand migration, scour, and deposition. The New Mexico Interstate Stream Commission (NMISC) used the FLO-2D (Tetra Tech, Inc., 2002) flood routing model developed for the Middle Rio Grande to develop hydrographs for each release and collection site in 2005. Measured 60-min flows from USGS gages for the Rio Grande at San Felipe (#08319000) and Jemez River below Jemez Dam (#08329000) were used as initial input to the model.

Mussetter Engineering, Inc. (MEI) developed flow hydrographs for each site in 2007 using the updated 76.25-m grid resolution FLO-2D model (Riada Engineering, Inc. [Riada], 2008). Inflow and outflow hydrographs developed from analysis of the USGS and Middle Rio Grande Conservancy District (MRGCD) gage records were input to the FLO-2D model. This model was further calibrated using the elevation of high water marks collected in 2005 and aerial photography and flood mapping by the U.S. Army Corps of Engineers from 2005. Both the NMISC and MEI FLO-2D models produced instantaneous discharge estimates in 1-h intervals for each release and collection site, which were subsequently reduced to 15-min intervals assuming a linear change in discharge each hour.

Calculation of Reach-Specific Bead Retention

The number of beads passing a collection site during 5 d, and the percentage of beads released that did not pass a collection site in 5 d was assumed to have been retained upstream of that point (Medley *et al.*, 2007). Five days represents maximum time that eggs and larvae passively drift before larvae begin to actively seek suitable rearing habitat (Platania and Altenbach, 1998).

The expansion of 15-min estimates of bead passage through the channel to 5-d bead passage estimates followed the methods of Medley *et al.* (2007). The number of beads that passed each site during the field collection period (i.e., 1-2 d) was estimated from the field data as the sum of the number of beads passing a given collection site in each 15-min period. The number of beads that passed each site from the end of the collection period to day 5 was intentionally overestimated by holding the collection rate at the end of the field collection period constant through day 5. A constant rate of bead passage was used rather than a decaying rate during this period so that bead retention would be underestimated. We felt that an underestimate of retention supported a conservative approach to conservation planning.

The number of beads passing collection sites was analyzed using a simple empirical model that assumed a negative exponential decay between release and collection sites (Equation 1). This model was used to calculate the instantaneous bead retention rate (r) between sites:

$$Beads(x+\Delta x) = Beads(x)e^{-r\cdot\Delta x} \qquad (1)$$

Where: $Beads(x+\Delta x)$ = number of beads reaching the bead collection site at river kilometer $x + \Delta x$; $Beads(x)$ = number of beads entering the reach at river kilometer x; r = bead retention rate (1/km); and Δx = distance traveled to the next downstream collection site (km) (Medley *et al.*, 2007). The negative sign on the retention rate (r) indicates a decrease in beads per kilometer, or the rate at which beads are retained and lost from the population moving downstream. The discrete model loss (rd) describes the proportion of beads retained per kilometer (%/km) (Equation 2):

$$rd = e^{-r} - 1 \qquad (2)$$

Bead retention calculations for the Isleta Reach during experiments 4 and 5 were corrected for diversion of beads from the channel into irrigation canals by the Isleta Diversion Dam, assuming a uniform mixture of beads in a volume of water. Before calculating retention between SDC and San Acacia, the 5-d bead passage estimate at San Acacia was increased by the mean proportion of the river discharge (%) diverted at Isleta Diversion Dam for the field data collection period (i.e., 12.4% and 15.2% for experiments 4 and 5, respectively). The proportion of flow diverted was determined by Mussetter Engineering, Inc. using the FLO-2D model (Riada, 2008).

Model of Silvery Minnow Egg Retention

A spreadsheet model was used to estimate cumulative retention of eggs in the Albuquerque and Isleta reaches assuming that eggs were released in the open channel in proportion to the documented distribution of adult silvery minnow population, rather than at a point location. The total number of eggs retained in each reach was modeled as a function of the per-km egg retention rate (r) and the longitudinal distribution of adult spawning silvery minnow in 2005. We used the spreadsheet model and methods developed by Medley *et al.* (2007) to predict downstream egg transport in 1-km increments and to estimate cumulative silvery minnow egg retention in the Albuquerque and Isleta reaches over a 5-d period. The approximate breeding distribution of the silvery minnow was derived from catch per unit effort data (fish per 100 m^3) collected in April, May, and June 2005 (Dudley *et al.*, 2005a), (Dudley *et al.*, 2005b), (Dudley *et al.*, 2005c). For experiments 1, 3, and 6, the river section between SDC and Isleta Diversion Dam was assumed to have the same retention rate as the section between Angostura Diversion Dam and SDC (i.e., the Albuquerque Reach was assigned a single rate). For experiments 4 and 5, the retention rate changed between reaches at SDC, where we had collected the bead data. Results from experiment 1a were used rather than results from experiment 1 in the Isleta Reach because more data were available.

Bead Velocity at Discharge

Bead velocity (km/h) was calculated as the distance traveled between the time of bead release and the time of peak bead density observed at a downstream collection site. The first bead was usually collected 15–60 min before peak bead density. Maximum bead density was used so that the calculated velocity would describe the movement of the majority of beads. Measured bead velocities were compared to those predicted by the reach- and discharge-specific models of Dudley and Platania (2007), and tested for a relationship between bead velocity and bead retention (n = 9) by linear regression.

RESULTS

Peaks in bead density were observed at collection sites within 3 h after the initial arrival of the first beads, and bead density decreased rapidly to low levels for the remainder of each experiment (Figure 3). The peaks became more rounded as more beads were retained, either because the site was further from the point of bead release or because the rate of retention was high. An anomalous pattern in bead density occurred during experiment 5 at the San Acacia collection site where two peaks in bead density were observed; a second smaller peak occurred concomitant with an abrupt 6 m^3/s increase in flow caused by unusual Isleta Diversion Dam operations. Small numbers of wild silvery minnow eggs were collected indicating that the conditions in which the experiments were conducted coincided with a natural spawning event. Silvery minnow eggs were collected at the San Acacia collection site during experiment 1 (5.05 eggs/100 m^3 water), experiment 2 (11.98 eggs/100 m^3), and experiment 5 (0.004/100 m^3), and at the SDC collection site during experiment 4 (0.04/100 m^3).

Of the beads released below Angostura Diversion Dam, 2.60–22.50% were estimated to have passed the SDC collection site and 0–2.75% were estimated to have passed the San Acacia collection site in 5 d (Table 1), depending on hydrologic conditions. Of the beads released below

Isleta Diversion Dam, an estimated 0.02–1.80% passed the San Acacia collection site in 5 d. The number of beads passing San Acacia during experiment 5 may have been greater than would be expected with usual Isleta Diversion Dam operations.

Estimated rates of bead retention varied between reaches and among hydrologic conditions (Table 2). Within the same reach and year, retention was consistently higher during the high ascending flow than during the high or low descending flow or during the stable flow. At the higher bead retention rates observed, more than 90% of beads were predicted to be retained within 50 km of their origin (Table 2), which is shorter than either of the Albuquerque (67 km) and Isleta (86 km) reaches. At the lowest observed rates, more than 75% of drifting beads would be retained within 83 km of their release point and more than 90% within 137 km.

The spreadsheet model of cumulative egg retention applied the bead retention rates estimated in Table 2 to the population distribution recorded for silvery minnow in spring 2005. Assuming eggs are produced in proportion to fish density, the silvery minnow population distribution between Angostura and San Acacia diversion dams indicates that 22% of eggs in this section are produced in the Albuquerque Reach and 78% are produced in the Isleta Reach. The model predicted that 39–63% of eggs produced in the Albuquerque Reach are retained upstream of Isleta Diversion Dam (Figure 4). However, these eggs represent only 8–14% of the eggs produced in the Albuquerque and Isleta reaches combined (Figure 5). The model predicted that 50–96% of eggs produced in the Isleta Reach are retained upstream of San Acacia Diversion Dam. Eggs retained in the Isleta Reach represent 49–83% of the eggs produced in the Albuquerque and Isleta reaches combined. Cumulatively, 58–96% of eggs produced in the Albuquerque and Isleta reaches were predicted to have been retained upstream of San Acacia Diversion Dam at the range of flows tested in 2005 and 2007.

Bead velocity ranged from 2.06–3.84 km/h in the Albuquerque Reach and 2.92–3.66 km/hr in the Isleta Reach for the range of flows tested (Table 2). Bead velocities were 5% higher on average in the Albuquerque Reach and 16% higher in the Isleta Reach than predicted by Dudley and Platania's (2007) reach-specific particle transport models. No statistically significant relationship was detected between bead velocity and bead retention (linear regression, n = 9, adjusted $R^2 = 0.205$, $P = 0.123$).

DISCUSSION

Bead experiments demonstrated that Rio Grande silvery minnow egg and larval retention can be high in the Middle Rio Grande under the range of snowmelt runoff flows that currently occur and in which the silvery minnow is known to spawn. Additionally, the results are consistent with the hypothesis that silvery minnows may release eggs during rapidly increasing flows to take advantage of flood attenuation and channel storage that limits downstream displacement of propagules (Medley *et al.*, 2007).

Retention of pelagic drifting particles measured during these seven experiments was higher than those previously reported for the Albuquerque and Isleta reaches (Dudley and Platania, 2007). Calculated retention rates indicate that 90% of particles released at a point will be retained within about 32–107 km in the Albuquerque Reach and 23–137 km in the Isleta Reach, depending on hydrologic conditions (Table 2). The range of these estimated retention rates suggests that transport distances of silvery minnow propagule could be less than 50% of the 216–359 km previously estimated in the 2003 Biological and Conference Opinions for Middle Rio Grande Water Operations (USFWS, 2003). The estimates of retention (r = 0.0168–0.1020) are in the range of those reported by Medley *et al.* (2007) in the Pecos River (r = 0.006–0.045), but substantially higher than measured by Dudley and Platania (2007) in the Middle Rio Grande (r = 0.0072).

Differences in bead type may have contributed to differences in measured bead retention. The gellan gum beads used in this study and by Medley *et al.* (2007) differed in size, shape, and texture from the nylon beads used by Dudley and Platania (2007), although their specific gravity was similar (Cowley *et al.*, 2005; Dudley and Platania, 1999). As a result, the two bead types may behave differently in a riverine environment and affect downstream transport. The gellan gum beads remaining in the drift traveled 5–16% faster on average than predicted by Dudley and Platania's (2007) reach-specific egg transport model, although we detected no relationship between bead velocity and retention rate. Gellan gum beads are similar in size, shape, texture, and specific gravity to silvery minnow eggs (Cowley *et al.*, 2005) and are expected to be retained by the same mechanisms that retain wild silvery minnow eggs.

This study demonstrated that differences in the magnitude and shape of a hydrograph and its relationship to the timing of bead release may explain some of the differences reported in measured retention rates. Dudley and Platania (2007) conducted a single drift experiment between Cochiti Dam and the Elephant Butte Reservoir where beads were released at stable high flow (102 m^3/s) in 2001. Our study quantified bead retention at a range of flows during the hydrologic conditions that stimulate silvery minnow spawning (i.e., ascending limb of a flood pulse [Platania and Altenbach, 1998]) and when flood attenuation and channel storage promote efficient egg retention.

Optimal egg retention appears to occur at different flows in the Albuquerque and Isleta reaches. Bead retention was greater in the Albuquerque Reach than in the Isleta Reach during all experiments in 2007, counter to bead retention rates observed in 2005 when flows were substantially higher (Table 2). Bead retention in the Albuquerque Reach was 1.1–2.3 times greater in 2007 than in 2005 for comparable points on the snowmelt hydrographs (i.e., low-flow descending limb and high-flow ascending limb, respectively). We hypothesize that medium-high flows, such as those tested in experiments 4 and 5 in 2005, are sufficient to inundate islands and other vegetated in-channel floodplain features that retain eggs in the Albuquerque Reach. In a series of smaller-scale experiments to characterize bead retention by habitat type, Porter and Massong (2006) documented highest retention of beads in flooded shoreline areas, especially shelves, and on flooded island and sand bar surfaces in the Middle Rio Grande. Overbank flooding occurs only at the highest expected flows in the Albuquerque Reach due to channel incision, so egg-retaining features may be rendered ineffective by high-velocity water at high river discharges, resulting in lower egg retention (e.g., experiment 1). Based on bead retention rates, the interaction of river discharge, channel complexity, and river-floodplain connectivity is greater in the Isleta Reach, where there is less degradation of the channel and overbank flooding occurs intermittently from levee to levee during moderate to high flows.

Highest bead retention in the Isleta Reach occurred on the rising limb of a high magnitude hydrograph, coincident with a period of substantial overbank flooding (experiment 1). Retention in the Isleta Reach was 2.1 times greater during experiment 1 than experiment 2, which occurred at a comparable flow magnitude without overbank flows, and 2.3 times greater than during experiment 4, which also occurred after a flood pulse but at a lower flow magnitude. Bead retention during experiment 1 was 3.3 times greater in the Isleta Reach than in the Albuquerque Reach, where no overbank flooding occurred. Although the physical mechanisms of egg retention were not specifically evaluated by this study, the extremely high retention associated with floodplain inundation in the Isleta Reach supports previous findings suggesting that egg retention is habitat dependent (Medley *et al.*, 2007).

Reaches with high habitat heterogeneity and complex channel structure consistently have slower rates of bead drift (Dudley and Platania, 2007) and higher rates of retention (Medley *et al.*, 2007) than channelized reaches with more homogenous habitat. Pease *et al.* (2006) found highest densities of silvery minnow larvae in backwater habitats, available only after high flow events and in isolated pools. The relationship between discharge and habitat availability is dependent on channel morphology. Greatest reproductive success and larval survival may not occur at the highest flow, but at the flows that maximize habitat heterogeneity and availability for young of year fish (Moore and Thorp, 2008). Models of habitat availability at discharge can be used to elucidate large-scale habitat-related egg retention mechanisms and spatial relationships between potential egg-retaining habitats and persistent larval/juvenile fish habitats for each reach. These analyses of reach-specific egg retention and a better understanding of flow to habitat relationships can help to better inform flow management and habitat restoration to benefit silvery minnow recruitment.

Spawning after a flood pulse may also enhance egg retention. In both the Albuquerque and Isleta reaches, bead retention was greater just after a flood pulse during the ascending limb of the snowmelt hydrograph than during the descending limb of the hydrograph in the same year. While differences in flow magnitude and extent of floodplain inundation among experiments confounded direct comparisons of retention between ascending and descending limb hydrographs, the results were consistent with the hypothesis proposed by Medley *et al.* (2007); i.e., spawning on the ascending limb of the hydrograph is a reproductive strategy to limit downstream displacement of propagules which are stored in the channel concomitant with flood attenuation and channel storage. Spawning during this time confers a reproductive advantage over eggs transported farther downstream and avoids the need for energetically costly upstream migrations. The flood wave originating upstream becomes protracted with a reduced flow peak as water entering channel storage is subsequently released to downstream reaches (Price, 1985; Chow *et al.*, 1988). Drifting eggs also enter channel storage as the channel fills (Medley *et al.*, 2007). The time that propagules spend in channel storage depends on channel morphology; a connected floodplain allows for more rapid and greater water storage as it is inundated, resulting in a more attenuated and delayed flood wave (Price, 1985; Chow *et al.*, 1988). Theoretically, releases from Cochiti Reservoir timed to coincide with appropriate water temperatures (16-27°C [Platania, 1995]) could both stimulate silvery minnow spawning and shorten egg drift distance via channel storage of water. Sufficient time in channel storage would allow larvae to reach the metalarval stage of fin development and gain the ability to resist further downstream transport.

Highest egg retention rates were observed in the Isleta Reach, which has a larger adult population and a greater amount of habitat complexity and floodplain inundation than the Albuquerque Reach. Silvery minnow population distribution and reach length also affected cumulative egg retention within a reach. The Albuquerque and Isleta reaches are approximately 67 and 86 km long, respectively, so each could retain a high proportion of silvery minnow eggs over the full range of flows tested if the fish were concentrated toward the upstream end of each reach. It is important to retain a proportion of the eggs upstream of the diversion dams because the dams restrict upstream movement of juvenile and adult fish. The model of cumulative egg retention estimated that less than 63% of silvery minnow eggs spawned in the Albuquerque Reach would be retained upstream of Isleta Diversion Dam based on the 2005 silvery minnow spring population distribution, which appeared to be concentrated in the lower segments of the Albuquerque Reach near Isleta Diversion Dam (Figure 4). The model indicated much higher retention in the Isleta Reach (50–96% of eggs), even at comparable per-km retention rates, because the Isleta Reach is longer and because the silvery minnow population was estimated to be concentrated in the upstream half of the reach in spring 2005 (Figure 4).

Because cumulative egg retention in the Isleta Reach (49–83%) is predicted to be substantially higher than cumulative egg retention in the Albuquerque Reach (8–14%), habitat restoration efforts should be focused in the Albuquerque Reach. Restoration activities that will enhance retention include reconfiguration of mid-channel islands, bank destabilization, and reconnection of floodplains. The objective of these restoration activities is to provide habitat for all life stages of silvery minnow so that each reach can support a self-sustaining population. Flow intermittency, which is common in the Middle Rio Grande, is less likely in the upper sections of the Albuquerque Reach, and eggs released in these sections have better odds of retention upstream of Isleta Diversion Dam given the available drift distance. Recruitment can be further improved by increasing the availability of low velocity habitats that retain eggs (Porter and Massong, 2006) and providing nursery habitat for larvae and juveniles (Pease *et al.*, 2006). Restoration that occurs at the upstream end of the silvery minnow range would be more effective for species conservation if coupled with silvery minnow population augmentation by stocking or translocation.

Habitat restoration has already been initiated in the Middle Rio Grande. A non-inclusive list of work to date in the Albuquerque Reach includes 4.9 ha modified by the Bureau of Reclamation in 2005; 65.9 ha modified by the NMISC, impacting 121.2 ha between 2006 and 2007; and 10.7 ha modified by the City of Albuquerque in 2007 (SWCA Environmental Consultants, 2008). One habitat restoration project also occurred in the Isleta Reach in 2002. During restoration, bank surfaces were mechanically lowered to improve floodplain connection to the river, inundate floodplain habitats at lower flows, and increase habitat diversity by the creation of low-velocity habitats.

The effectiveness of habitat restoration will need to be closely monitored. Habitat requirements of the silvery minnow are not well known, particularly the locations and conditions in which spawning occurs (e.g., in the open channel or on the floodplain) and the environmental factors that maximize juvenile recruitment (Cowley *et al.*, 2006; Cowley, 2006). Silvery minnow larvae are most abundant in habitats with little or no flow and relatively high water temperature (Pease *et al.*, 2006). The suitability of habitats for larval fish is additionally influenced by water chemistry, zooplankton and phytoplankton densities, absence or presence of predators, algal and macrophyte densities, substrate, temporal stability, and longevity (Floyd *et al.*, 1984; Harvey, 1987; Scheidegger and Bain, 1995; Robinson *et al.*, 1998; Zeug and Winemiller, 2007; Zeug and Winemiller, 2008; Moore and Thorp, 2008). An adaptive management approach to habitat restoration has been adopted in the Middle Rio Grande where the results of monitoring are used to help direct future restoration efforts.

Based on the results of this study, habitat restoration to improve egg retention is most needed in the in the Albuquerque Reach. Restoration should increase inundation of in-channel and channel margin floodplain habitats in the contemporary range of spring flows and create persistent larval/juvenile fish habitats. A single flow may not maximize spawning and nursery habitat of silvery minnow in all reaches. Reach-specific relationships of flow to habitat should be developed to elucidate habitat-related mechanisms of egg retention and to better understand where the population of silvery minnow will most benefit from a given flow. In addition to habitat restoration, spring water releases from Cochiti Reservoir could be timed to stimulate silvery minnow spawning and to shorten egg drift distances through channel storage of water. The quality and duration of nursery habitat may limit the survival of those eggs/larvae retained, so the effectiveness of flow management and habitat restoration to improve young-of-year survival will need to be closely monitored.

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Table 1. Numbers of beads released below Angostura Diversion Dam (ADD) and Isleta Diversion Dam (IDD) and collected near the Southern Diversion Channel (SDC, 51 RK downstream) and San Acacia (SA, 149 RK downstream), expanded estimates of channel-wide bead passage, and estimates of 5-d passage. Dashes (–) indicate that beads were not released at that site or the site was not sampled.

Experiment Number (Bead Release Time)	Bead Sampling Period	Beads Released		Beads Collected		Estimated Beads that Passed During Sampling		Estimated Total Beads Passed in 5 d (% of Total Released)	
		ADD	IDD	SDC	SA	SDC	SA	SDC	SA
1 (May 12, 2007 07:08)	May 12, 2005 15:45 to May 14, 2005 18:15	10,140,000	–	548	0	2,037,097	0	2,037,182 (20.1%)	0 (0%)
1a (May 12, 2005 16:19)	May 13, 2005 04:00 to May 14, 2005 18:15	–	10,140,000	–	1	–	1,990	–	1,990 (0.02%)
2 (June 22, 2005 08:40)	June 23, 2005 05:00 to June 25, 2005 01:15	–	10,140,000	–	175	–	186,651	–	186,655 (1.8%)
3 (July 7, 2005 06:20)	July 7, 2005 16:30 to July 8, 2005 21:45	10,140,000	–	3,021	–	1,809,005	–	2,278,481 (22.5%)	–
4 (May 18, 2007 18:10)	May 19, 2007 05:15 to May 21, 2007 23:45	7,925,250	–	99	3	201,004	2,096	206,332 (2.60%)	2,096 (0.03%)
5 (May 29, 2007 19:21)	May 30, 2007 07:00 to June 1, 2007 23:45	7,925,250	–	1,409	248	1,196,658	176,855	1,291,058 (16.29%)	217,959 (2.75%)
6 (June 24, 2007 17:23)	June 25, 2007 07:30 to June 27, 2007 20:30	7,925,250	–	3,711	–	1,297,779	–	1,544,931 (19.49%)	–

Table 2. Bead velocity, instantaneous per-km bead retention rate (r), and distance to retain different proportions of sites downstream of a point release location in each reach (ABQ = Albuquerque; ILT = Isleta) based on data from the bead drift experiments at different river hydrographs and discharges (Q).

Hydrograph	Reach	Experi-ment	Mean Q at Bead Collection Site (m^3/s)	Velocity (km/hr) Based on Peak Bead Density	Retention Rate (r) (%/km)	Km Necessary to Retain Proportions (%) of Beads Downstream of the Release Site				
						10%	25%	50%	75%	90%
High flow ascending limb	ABQ	1	161	3.84	0.0313 (3.1%)	3.4	9.2	22.1	44.3	73.6
		4	97	3.58	0.0711 (6.9%)	1.5	4.0	9.7	19.5	32.4
	ILT	1a	140	3.66	0.1020 (9.7%) [a, b]	1.0	2.8	6.8	13.6	22.6
		4	98	3.03	0.0453 (4.4%)	2.3	6.4	15.3	30.6	50.8
High flow descending limb	ABQ	5	73	3.13	0.0353 (3.5%)	3.0	8.1	19.6	39.3	65.2
	ILT	5	67	2.92	0.0168 (1.7%)	6.3	17.1	41.3	82.5	137.1
		2	137	3.21	0.0477 (4.7%)	2.2	6.0	14.5	29.1	48.3
Low flow descending limb	ABQ	3	46	2.50	0.0215 (2.1%)	4.9	13.4	32.2	64.5	107.1
		6	22	2.06	0.0318 (3.1%)	3.3	9.0	21.8	43.6	72.4

[a] floodplain inundation occurred.

[b] based on beads released below Isleta Diversion Dam.

Figure 1. Study area in the Middle Rio Grande, New Mexico, USA.

Figure 2. Contemporary (1987–2007) range of mean daily discharge in May through July at the USGS Rio Grande at Albuquerque gage (08330000), and mean daily discharge during the seven bead drift experiments in 2005 (a) and 2007 (b).

Figure 3. Examples of typical patterns in bead passage from the SDC collection site during experiments 4, 5, and 6 in 2007.

Figure 4. Models of cumulative Rio Grande silvery minnow egg retention in the Albuquerque (a) and Isleta (b) reaches separately based on the spring 2005 estimated population distribution (from catch rates) and retention values calculated from the seven bead drift experiments. The Albuquerque Reach is bound by the Angostura and Isleta diversion dams and the Isleta Reach is bound by the Isleta and San Acacia diversion dams.

Figure 5. Model of cumulative Rio Grande silvery minnow egg retention in Albuquerque and Isleta reaches combined based on the spring 2005 estimated population distribution (from catch rates) and retention values calculated from the seven bead drift experiments.