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Review and reinterpretation of Rio Grande silvery minnow reproductive ecology using egg biology, life history, hydrology, and geomorphology information

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ABSTRACT

To inform management actions to recover the endangered Rio Grande silvery minnow (*Hybognathus amarus*, RGSM), we (1) calculated the terminal settling velocities of newly expelled and water-hardened RGSM eggs for the observed range of suspended sediment concentrations and water temperatures in the Rio Grande, New Mexico, USA, and (2) reviewed RGSM reproductive ecology in the context of egg biology, the species' life history, and the historic and contemporary hydrology and geomorphology of the Rio Grande. Results show that in a naturally functioning riverine environment, the location and timing of spawning, the ontogenic stage of egg development, and habitat-specific differences in sediment and temperature that influence egg-settling rates interact to (1) prevent egg suffocation, (2) promote egg entrainment in clear, warm, productive floodplain habitats, and (3) limit downstream population displacement. Our research suggests that the RGSM is primarily a demersal, floodplain spawning species that evolved eggs that are secondarily buoyant in high-sediment environments rather than a main channel, pelagic broadcast-spawning species with an evolved long-distance, downstream drift phase, as previously reported. The current high magnitude of egg drift is hypothesized to be an artefact of contemporary river management and channelization, leading to reduced lateral connectivity, floodplain abandonment, and habitat degradation. Conservation actions implemented to restore historic channel form and reconnect low-velocity backwater and floodplain habitats are recommended. In the absence of a documented upstream migration of adult fish, removal of barriers to a presumed upstream movement is unlikely to provide immediate benefits to RGSM. Copyright © 2013 John Wiley & Sons, Ltd.

KEY WORDS Rio Grande silvery minnow; reproductive ecology; life history; egg; demersal; pelagic; hydrology; geomorphology

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INTRODUCTION

In lowland floodplain rivers of western North America, a reproductive guild of small, broadcast-spawning minnow (BSM) species has evolved in hydrologically variable but seasonably predictable rivers. These minnows maximize their reproductive success by spawning in response to rapidly increasing flows associated with spring runoff and summer rainstorms (Platania and Altenbach, 1998). Members of this guild have declined dramatically as a result of a multitude of negative impacts (Bestgen and Platania, 1991; Platania, 1991) primarily driven by dam construction and water resource development and the attendant effects on hydrology, geomorphology, and river habitats (Lagasse, 1981; Ward and Stanford, 1995; Collier *et al.*, 1996; Dean and Schmidt, 2011; Swanson *et al.*, 2011). Many now occupy a small proportion of their former range, are listed as threatened and endangered under state laws and the federal Endangered Species Act, or extinct (Deacon *et al.*, 1979; Miller *et al.*, 1989; Williams *et al.*, 1989; Haslouer *et al.*, 2005). Accordingly, these species are the focus of intensive efforts to resolve the conflicts between water resource management and species conservation (Edwards and Contreras-Balderas, 1991; Ward and Booker, 2003; Cowley, 2006; Ward and Booker, 2006; Ward and Pulido-Velázquez, 2008), including research efforts to better understand the management actions that will promote their recovery (Medley, 2009).

The reproductive strategies and egg types of seven Rio Grande Basin BSM species have been characterized (Platania and Altenbach, 1998). Six, including the federally endangered Rio Grande silvery minnow (*Hybognathus amarus*, RGSM; Figure 1), were reported to be 'pelagic broadcast spawners', fish that broadcast non-adhesive, semi-buoyant eggs (Figure 2) into the water column, which then drift downstream. The physical properties of RGSM eggs and the ontogenic phases of egg development have also been characterized (Platania and Altenbach, 1998; Cowley *et al.*, 2005, 2009). Furthermore, a considerable amount of published and unpublished information exists documenting RGSM spatial and temporal population trends, spawning periodicity, egg drift, and RGSM movement, and represents the most complete description concerning the reproductive ecology of any BSM. Consequently, the RGSM information, when considered with information about other BSM, perhaps provides the best model species to understand the general spawning ecology of this group of BSM species.

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Figure 1. Rio Grande silvery minnow; gravid female.

Figure 2. Water-hardened Rio Grande silvery minnow eggs.

The RGSM is a small BSM (<100 mm) native to the Rio Grande basin, including the Pecos River, with an original distribution from north central New Mexico (Cope and Yarrow, 1875) to the river's mouth in Brownsville, Texas (Girard, 1856). Currently, the species' known distribution is restricted to two river reaches amounting to less than 10% of its historic range. The extant range includes the remaining native population downstream of Angostura Dam near Albuquerque to Elephant Butte Reservoir in New Mexico (Bestgen and Platania, 1991) and a recently introduced experimental population in Big Bend National Park, Texas (U.S. Fish and Wildlife Service, 2008; Shirey and Lamberti, 2010).

EGG BIOLOGY AND LIFE HISTORY

RGSM spawn in late April and May during flood pulses or managed Cochiti Reservoir releases associated with spring snowmelt, when water temperatures exceed 18 °C (Sublette *et al.*, 1990; Platania and Altenbach, 1998; Propst, 1999; Platania and Dudley, 2005). After expulsion and fertilization, eggs may settle or drift suspended by turbulent flows. Newly expelled eggs are spherical and ~1·0 mm in diameter (Platania and Altenbach, 1998). Eggs rapidly water harden and swell to greater than 50 times their initial volume, becoming ~3·75 mm in diameter (Figure 2) with a density of 1·00281 g cm^{-3} after 1 h (Cowley *et al.*, 2005, 2009). Eggs have been observed drifting until they are entrained in low-velocity habitats (backwaters, channel edges, and floodplains) or hatch 24–72 h post-fertilization. Newly hatched larvae have also been reported to drift passively for another 3 days until their air bladders develop whereupon they are thought to actively seek low-velocity habitats (Platania and Altenbach, 1998).

Moore (1944) hypothesized that egg suspension and downstream drift during high flows evolved because it confers a reproductive advantage over substrate spawning by reducing egg suffocation (Johnston and Page, 1992). Consequently, RGSM and other BSM are hypothesized to be main channel, pelagic broadcast-spawning fish with an evolved long-distance downstream egg and larval drift phase as a core component of their life history strategy. In highly regulated and modified rivers with reduced floodplain connection, eggs have been observed to drift long distances downstream (>150 km) leading to speculation that RGSM and other BSM must undertake an upstream migration during their lifetime to counter the effects of downstream drift (Platania, 1995; Bestgen *et al.*, 2010). However, these presumed minnow migrations remain undocumented (Luttrell *et al.*, 1999; Medley *et al.*, 2007; PBS&J, 2011). Moore's hypothesis has led to the supposition that populations of BSM have declined because of dam construction and river fragmentation, which creates river reaches too short to accommodate the life history of these fish (Platania and Altenbach, 1998; Luttrell *et al.*, 1999; Dudley and Platania, 2007; Perkin and Gido, 2011; Archdeacon and Remshardt, 2012). Accordingly, the removal of irrigation diversions and other barriers to upstream movement or migration, or the construction of fish passageways to re-establish *longitudinal* connectivity, has been recommended as the primary conservation need for RGSM and other threatened BSM populations (Dudley and Platania, 2007; Perkin and Gido, 2011).

However, BSM populations still persist in fragmented and highly modified river reaches. Alternatively, other studies have concluded that BSM species that spawn on the rising limb of a flood hydrograph take advantage of egg retention mechanisms associated with channel storage and flood attenuation that promotes entrainment and settling of drifting eggs in areas of low-velocity flow near spawning sites (Fluder *et al.*, 2007; Medley *et al.*, 2007; Medley, 2009; Medley *et al.*, 2009; Widmer *et al.*, 2012). These species may further enhance egg retention by spawning in remnant low-velocity river channels or inundated floodplain habitats (Gonzales *et al.*, 2012) when available. Efficient egg retention limits downstream displacement of BSM populations and perhaps increases reproductive success by avoiding the need for energetically expensive upstream migrations (Hirshfield and Tinkle, 1975; Speirs and Gurney, 2001; Medley *et al.*, 2007). This hypothesis proposes that the contemporary high magnitude of downstream egg drift is an artefact of the geomorphic and habitat changes that accompany dam construction and flow regulation and the subsequent reduction in low-velocity river and floodplain habitats; short reaches of river that retain remnants of functional habitat features may still promote efficient egg retention sufficient to support healthy BSM populations (Medley *et al.*, 2007; Widmer *et al.*, 2012). Consistent with this hypothesis, conservation actions that help restore the geomorphic functions and processes that create and maintain the natural channel form and re-establish *lateral* floodplain connectivity are considered the primary conservation need (Medley, 2009; Magana, 2012).

The interpretation of recent observations regarding RGSM and BSM spawning behaviour is confounded because the habitat in the contemporary Rio Grande and other large floodplain rivers has been severely altered (Benke, 1990; Crawford *et al*., 1993; Scurlock, 1998; Dean and Schmidt, 2011). Life history strategies of BSM that either prevent downstream population displacement or subsequently compensate for downstream egg drift may operate synergistically. However, in the highly modified contemporary Rio Grande, the relative contribution of each strategy and the ultimate cause of the current imbalance between the observed magnitude of egg and larval drift and upstream fish movement or migration remains unresolved. The consequences of getting the science wrong may be costly in both money and loss of support for endangered species research and recovery. With tight government budgets and difficult choices on the number and scope of management actions that can be funded, scientists must identify the correct cause and effect relationships using the best available science and implement appropriate conservation measures to effectively recover species. A more complete understanding of BSM egg biology and BSM life history strategies is needed to better inform such management decisions.

Eggs of BSM settle in non-turbulent water (Platania and Altenbach, 1998; Cowley *et al*., 2005, 2009). The rate at which a spherical minnow egg settles (or rises) in a still medium is dependent on the size and density of the sphere, the density and viscosity of the medium (the latter being temperature dependent), and how these variables affect the relative magnitude of the three forces acting on the egg in suspension; gravity, buoyancy, and drag (friction). The magnitude of the downward force is a consequence of gravity acting on the mass of the egg. The magnitude of the upward acting force of buoyancy is dependent upon the mass of the fluid medium displaced by the egg. Settling occurs when the downward force of gravity acting on an egg exceeds the upward force of buoyancy. The terminal settling velocity is reached when the drag force exactly opposes the net downward force acting on the egg. When the density of the medium is greater than the density of the egg, the sphere will rise and float. The terminal settling velocity of silvery minnow eggs is therefore dependent upon the size and density of the egg and the temperature and sediment concentration of river water.

Recent observations that RGSM utilize and likely spawn in seasonally flooded habitats connected to the main channel (SWCA Environmental Consulting, 2008, 2009, 2010, 2010, 2011; Gonzales *et al*., 2012) suggest that their eggs may be subjected to a wide variation of temperatures and suspended sediment concentrations known to exist within these environments. Egg settling rate varies as a function of temperature, sediment concentration, and the ontogenic stage of egg development (Cowley *et al*., 2009). The hydrobiology of the RGSM egg suggests a complex but predictable relationship between egg properties, the physical properties of water, and the abundance and availability of different aquatic habitat types that create spatiotemporal variability in suspended sediment concentrations and temperatures in the floodplain and main channel. It is hypothesized that this environmental variability can influence the rate and magnitude of egg settling and retention. Understanding the biology of silvery minnow eggs may provide insight into RGSM and BSM adaptations to the heterogeneous environment of the historic Rio Grande. The magnitude of historic habitat alterations (Mussetter Engineering, Inc, 2002) also suggests that the contemporary state of the Rio Grande is a poor model for understanding the evolutionary pressures that have driven RGSM life history. Therefore, a review of the species' reproductive ecology in context with the historic geomorphology of the Rio Grande is necessary to inform effective management actions to recover the endangered RGSM.

We use available data to calculate the terminal settling velocity of newly expelled and water-hardened RGSM eggs in habitats with no flow velocity for a range of sediment and temperature conditions observed in the Rio Grande. Differences in egg-settling velocity may have important ecological consequences on egg drift and retention, egg survival and hatching, and young-of-year survival and recruitment. These results are used to explore the possible interactions between egg-settling velocity, egg properties, sediment concentrations, temperatures, and habitat availability. We then reinterpret the RGSM reproductive ecology on the basis of egg biology, historic Rio Grande geomorphology, RGSM life history, and recent observations suggesting that demersal spawning in low-velocity main channel and floodplain habitats is consistent with what is known about the reproductive ecology of other species of *Hybognathus* and other BSM.

CALCULATION OF EGG-SETTLING VELOCITY

Terminal settling velocities of newly expelled and water-hardened RGSM eggs were calculated at suspended sediment concentrations and water temperatures observed in the main channel and floodplain of the Rio Grande using Stokes' law:

$$v_{\mathrm{t}} = \sqrt{\frac{(\rho_{\mathrm{s}} - \rho_{\mathrm{f}})}{\rho_{\mathrm{f}}} \; \frac{g}{C_{\mathrm{D}}/2} \; \frac{V}{A}} \qquad (1)$$

where v_{t} is the terminal settling velocity ($\mathrm{cm\,s^{-1}}$), ρ_{s} the density of the sphere ($\mathrm{g\,cm^{-3}}$), ρ_{f} the density of medium ($\mathrm{g\,cm^{-3}}$), g the acceleration due to gravity ($\mathrm{cm\,s^{-2}}$), C_{D} the drag coefficient, V the volume of sphere [$4/3\pi r^3$ ($\mathrm{cm^3}$)], and A the cross-sectional area of the sphere [πr^2 ($\mathrm{cm^2}$)].

For large particles, drag is a function of the settling velocity. Because settling velocity and drag are interdependent, there is no easy analytical solution to determine settling velocity of a large sphere. The standard iterative approach was used to calculate egg-settling rates for newly expressed and water-hardened eggs at suspended sediment concentrations (0–150 000 mg l^{-1}) and temperatures (18 and 30 °C; reflecting silvery minnow minimum spawning temperatures and near maximum floodplain temperatures, respectively), observed in the Rio Grande (SWCA Environmental Consulting, 2009). At expulsion, RGSM eggs are spherical and ~1·0 mm in diameter (Platania and Altenbach, 1998). Water-hardened eggs are ~3·75 mm in diameter with a density of 1·00281 g cm^{-3} (Cowley *et al.*, 2005, 2009). The density of newly expelled eggs has not been determined but was backcalculated as 1·14818 g cm^{-3} using the reported properties of water-hardened eggs (Cowley *et al.*, 2009), assuming that egg swelling is dependent only on the passive movement of water through a semi-permeable membrane in response to an osmotic gradient.

The simplified form of Equation (1) for small particles was used to make an initial estimate of the terminal egg-settling velocity:

$$v_t = \frac{g\ D^2}{18\mu}(\rho_s - \rho_f) \tag{2}$$

where μ is the dynamic viscosity (g cm^{-1}·s^{-1}) and D the particle diameter (cm).

This initial estimate of v_t was used to derive an estimated Reynolds number (*Re*) for a settling egg:

$$Re = \frac{v_t\ \rho_f\ D}{\mu} \tag{3}$$

The Reynolds number was then used to estimate a drag coefficient using the general equation of Cheng (2009):

$$C_D = \frac{24}{Re}(1 + 0.27Re)^{0.43} + 0.47\left[1 - \exp\left(-0.04Re^{0.38}\right)\right] \tag{4}$$

The drag coefficient estimate was used to calculate settling velocity using Equation (1). The new estimate of settling velocity (v_t) was used to recalculate the estimated Reynolds number and the calculation process repeated until terminal settling velocity converged to a constant. Water viscosity for the calculations was assumed to be dependent only on temperature and unaffected by interactions with suspended sediment at the concentrations considered (Woo *et al.*, 1988).

EGG SETTLING RATES

Newly expelled RGSM eggs were calculated to settle in clear (sediment concentration of 0·0 mg l^{-1}), non-turbulent water at 2·95 and 3·32 cm s^{-1} in 18 and 30 °C water, respectively (Figure 3). Settling velocities of larger, less dense water-hardened eggs decrease to 0·79 and 0·87 cm s^{-1} at 18 and 30 °C, respectively (Figure 4). Settling velocities decrease to zero as sediment concentrations increase to the point at which egg density equals the density of the water sediment mixture. Newly expelled RGSM eggs become positively buoyant and float (calculated negative settling velocity) when sediment concentrations exceed egg density (>148 180 mg l^{-1}), whereas water-hardened eggs float at sediment concentrations greater than 2810 mg l^{-1}. For a specific egg size and density, eggs will settle faster in clear versus sediment-laden water and faster in warm versus cold water.

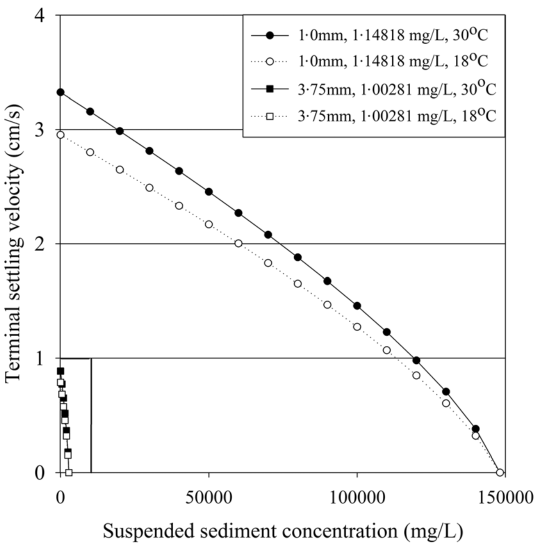

Figure 3. Relationships between terminal settling velocity (cm s^{-1}), sediment concentration (mg l^{-1}), and water temperature (°C) for newly expelled RGSM eggs (egg diameter = 1·00 mm, density = 1·14818 g cm^{-3}).

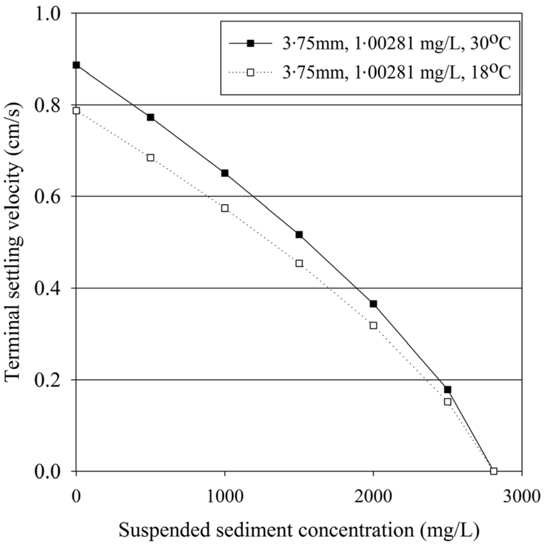

Figure 4. Relationships between terminal settling velocity (cm s^{-1}), sediment concentration (mg l^{-1}), and water temperature (°C) for water-hardened (more than 1 h old) RGSM eggs (egg diameter = 3·75 mm, density = 1·00281 g cm^{-3}).

The results support the general conclusions of other authors that both newly expelled and water-hardened RGSM eggs will settle in non-turbulent water except in high concentrations of suspended sediment (Platania and Altenbach, 1998; Cowley *et al.*, 2009). Our calculations show that recently spawned, small, dense RGSM eggs can settle out quickly in warm, low-velocity habitats with little suspended sediment. Results also confirm that water-hardened eggs will sink slowly in low sediment environments but are easily suspended and become positively buoyant in high concentrations of suspended sediment observed in the Rio Grande (Cowley *et al*., 2009).

Results suggest that egg-settling rates may be highly variable in a natural river environment with high spatial variability in sediment and temperature. During the high spring flows when RGSM spawn, suspended sediment concentrations in the main channel increase orders of magnitude over those observed at base flow as fine sediments from tributaries and the channel bed are mobilized (Graf, 1971). A small dataset documents the range of suspended sediment concentrations in the Rio Grande near Bernardo [U.S. Geological Survey (USGS) Gage 08332000] prior to the closure of Cochiti Dam (Figure 5). Suspended sediment concentrations during high spring flows in May and June when RGSM spawn exceeded that necessary to float a water-hardened (2810 mg l^{-1}) egg 59·0% of the time, but newly expelled eggs sank at all but the single maximum sediment concentration (167 000 mg l^{-1}) observed during the spawning season, for the period of record. No data are available documenting the spatial variability of floodplain sediment concentrations in the contemporary Rio Grande, although water clarity within the floodplain, especially at the floodplain margins and in areas of low velocity, is often much clearer than water clarity in or near the main channel (authors' personal observation). A recent dataset shows that water temperatures vary widely in the contemporary Rio Grande and temperatures in floodplain margins and pond habitats may exceed 30 °C (SWCA Environmental Consulting, 2009). During snowmelt runoff in the Rio Grande, water temperatures in the mainstem stay relatively cool.

Water-hardened RGSM eggs are buoyant in high-sediment environments. Therefore, it is unlikely that they can be suffocated by sediment as previously reported (Moore, 1944; Platania and Altenbach, 1998). As fine sediments settle, a density gradient is created above the riverbed. An egg will be suspended in the water column at the point where the fluid density equals that of the egg (1·00281 g cm^{-3}). As sediments continue to settle, the density gradient of the water sediment mixture above the bed surface increases, but the egg will remain at its equilibrium point slightly above the bed surface. Consequently, fine sediments are unlikely to bury water-hardened eggs, contrary to previous reports. If, after initial entrainment the sediment concentration should increase, the egg will rise and potentially drift until again settling in a warm, low-sediment environment.

HABITAT HETEROGENEITY IN THE HISTORICAL RIO GRANDE

Historically, the river was wide and shallow (Figure 6), with a braided channel (Figure 7) and an extensive, low-elevation floodplain (2–4 km wide) (Crawford *et al*., 1993; Molles *et al*., 1998; Scurlock, 1998; Dean and Schmidt, 2011). In all but the driest years the river was seasonally

Figure 6. 'On the Rio Grande' near San Ildefonso, NM, 1905, showing a wide, braided, and shallow river. Edward S. Curtis. Courtesy Palace of the Governors Photo Archives (NMHM/DCA), 143730.

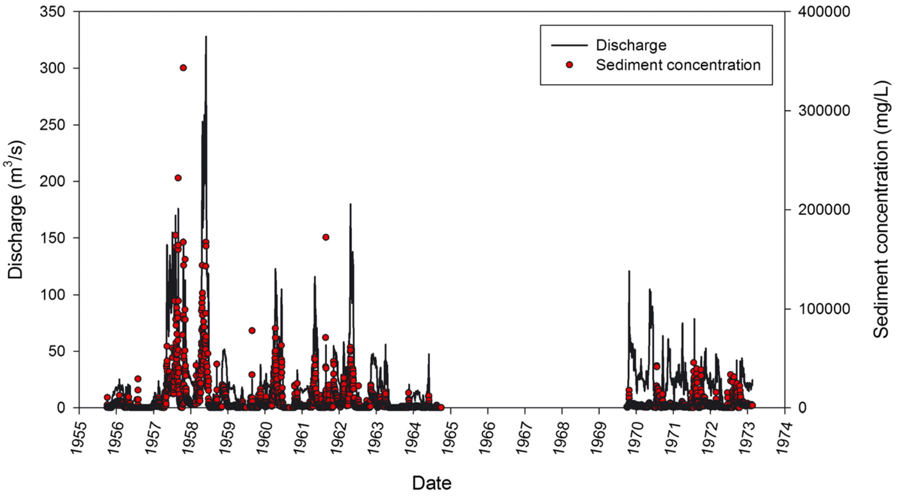

Figure 5. Discharge and suspended sediment concentrations at Rio Grande near Bernardo, NM (USGS Gage 08332000) prior to the closure of Cochiti Reservoir (1975).

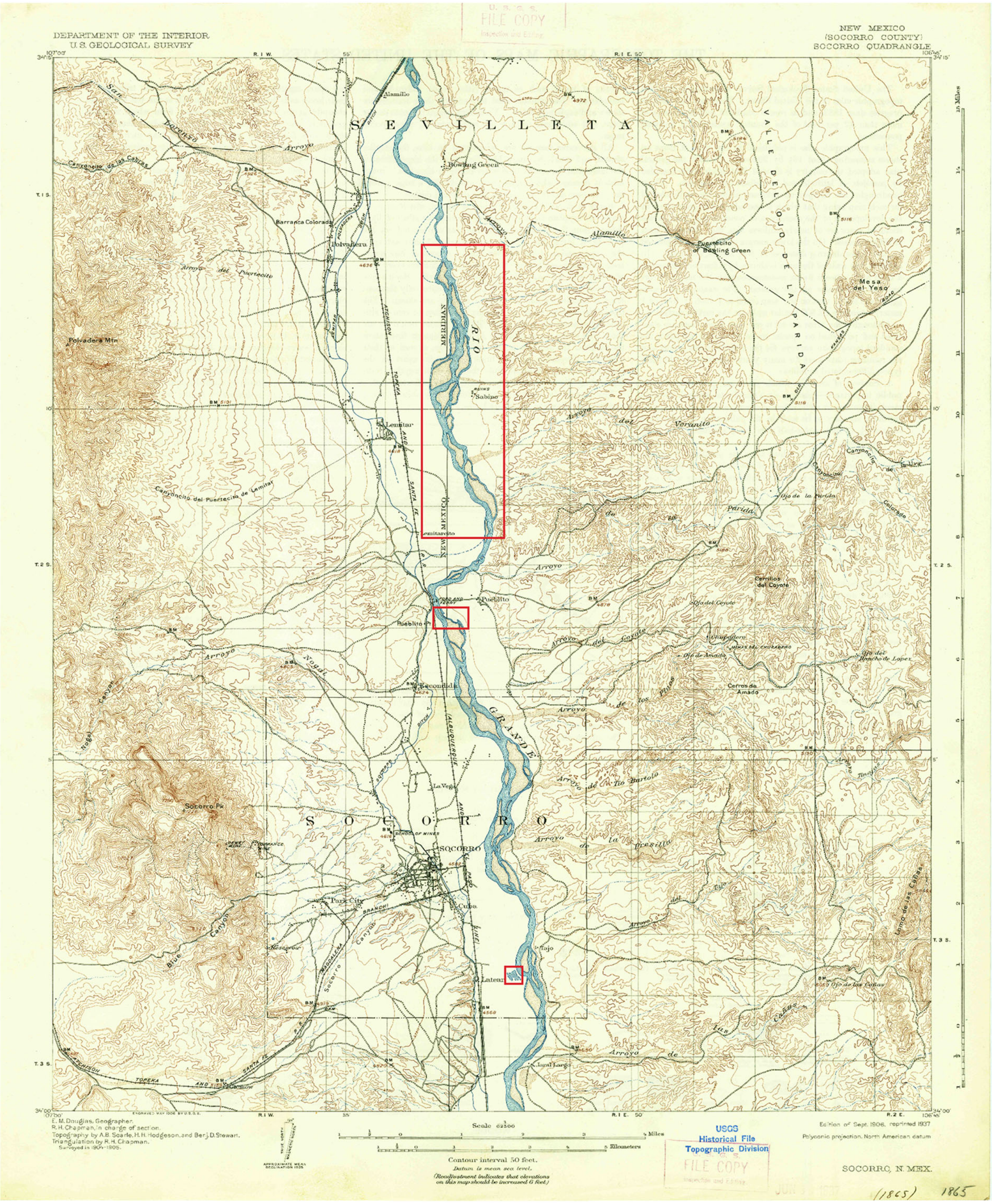

Figure 7. U.S. Geological Survey map of the Rio Grande near Socorro, NM, 1906, showing a wide braided channel that wandered within an extensive, connected floodplain. Habitat features highlighted from north to south include a braided river channel, a cutoff, and a floodplain lake.

connected to its floodplain which provided extensive low-velocity habitat for spawning fish and developing eggs and larvae (Figure 8). However, flow regulation, channel training and modification, removal of woody debris, sediment management, levee construction, lateral confinement and encroachment of non-native vegetation have changed the geomorphology of the Rio Grande (Lagasse, 1981; Sparks, 1995; Mussetter Engineering, Inc, 2002; Porter and Massong, 2004; Dean and Schmidt, 2011). The Rio Grande narrowed considerably between 1918 and 1962 as the river shifted from historical braided conditions to a narrow and deep channel disconnected from the floodplain (Swanson *et al*., 2011) (Figures 9–11). This greatly decreased the availability and diversity of habitat types.

To establish that environmental heterogeneity is a potential selective pressure in the evolution of RGSM reproductive ecology we should provide evidence that

Figure 8. Aerial photograph looking southwest showing braided channel and broad, inundated floodplain with lake-like conditions along Rio Grande near San Marcial, NM, 27 May 1937. E. D. Eaton. Reproduced by permission of New Mexico State University Library, Archives and Special Collections.

Figure 9. Rio Grande at Central Avenue, Albuquerque, NM, 1933, showing wide, braided channel. Reproduced by permission of the Middle Rio Grande Conservancy District.

spatial variation in sediment and temperature was present in the historical Rio Grande and that RGSM used these habitats. Although documentation of spatial patterns in temperature and sediment in the Rio Grande is limited, historical accounts and studies from less degraded and morphologically intact rivers may suggest how the unconstrained Rio Grande may have functioned. In contrast with the contemporary Rio Grande, rivers with braided channels are complex, heterogeneous systems that change yearly as floods shift fine sediment and new sediment is deposited (Warburton *et al*., 1993). In addition to differing rates of flow velocity and sediment in adjacent habitats, braided rivers with extensive floodplains can have a diversity of thermal regimes and geomorphology, even across transects perpendicular to the river channel (Mosley, 1983; Junk *et al*., 1989; Bayley, 1995). In the braided Tagliamento River, Italy, backwaters and pools formed in cutoffs connected to the main and side channels where current velocities of $0{\cdot}00\,\mathrm{m\,s^{-1}}$ have been measured, indicating stationary water (Arscott *et al*., 2001). The

Figure 10. Contemporary view of Rio Grande at Central Avenue, Albuquerque, NM, 2010, 77 years after Figure 9, showing the narrowing and stabilization of the river channel following extensive river training and the closure of Cochiti Reservoir (1975). Reproduced by permission of Dagmar Llewellyn.

observation of reduced flow velocity and stationary water in backwaters and pools adjacent to the main channel is explained by hydrodynamics (Nicholas and McLelland, 1999; Sutton *et al*., 2004). For example, a combination of field monitoring and simulation of flow velocities in the River Culm, UK, showed how flow dynamics in backwater pools of cutoffs from former channels resulted in high rates of sediment deposition during overbank flooding (Nicholas and McLelland, 1999). We expect that the same processes shown to retain sediment would also retain RGSM eggs, especially if RGSM spawn in these habitats with stationary water.

Historically in the Rio Grande, high flows also produced backwater habitat within the main channel, inundated the floodplain, and filled wetlands, oxbow lakes, and sloughs in former channels (Lee, 1907). For example, a USGS map of the Socorro reach in 1906 shows a braided river with side channels, a floodplain lake, and a cutoff or slough from a former channel (Figure 7). Further onto floodplains, water clarity increases and suspended sediment concentration is reduced as sediments settle (Gourley, 2001; Malard *et al*., 2006). Water temperatures are often considerably higher beyond the main channel as residency time increases (Mosley, 1983; Tockner *et al*., 2000; Arscott *et al*., 2001; Gourley, 2001).

Adult RGSM used these low-velocity habitats prior to major modification of the river channel (Shirey *et al*., 2008). Minnows collected in August 1874 in pools adjoining the Rio Grande at San Ildefonso, NM (Cope and Yarrow, 1875) had a dominance of nutrient-loving epipelic diatom species, other algae, and detritus in their gut contents. The presence of diatoms indicated the minnows foraged over a mud substrate consistent with a braided channel or lateral flooding and little ($<0{\cdot}2\,\mathrm{m\,s^{-1}}$) to no flow velocity (Cowley *et al*., 2006; Shirey *et al*., 2008). Habitats with these features include sloughs, side channels, and backwaters, which are consistent with habitats used by other *Hybognathus* (Raney, 1939; Copes, 1975; Goldowitz and Whiles, 1999; Scheurer *et al*., 2003). These laterally flooded habitats were gradually lost from the Rio Grande as a result of increasing flow regulation (Scurlock, 1998; Cowley, 2006; Dean and Schmidt, 2011); for example, riparian wetlands of the middle Rio Grande were reduced by 93% from 1918 to 1993 (21 052–1498 ha; Crawford *et al*., 1993).

Figure 11. Aerial photograph of Rio Grande Valley looking north towards Isleta and Albuquerque, from near Tome, NM, May 2011, showing the extent of historic floodplain and the contemporary Rio Grande channel, now channelized and straightened and constrained by jetty jacks and levees. Reproduced by permission of Dagmar Llewellyn.

MAGNITUDE OF DOWNSTREAM EGG DRIFT

The relative scarcity of floodplain and low-velocity habitats in the contemporary Rio Grande greatly reduces the opportunities for egg retention. Consequently, eggs and newly hatched larvae may drift considerable distances downstream before being entrained (Dudley and Platania, 2007; Widmer *et al*., 2012). BSM eggs have also been observed drifting in the main channel during summer floods and reservoir releases in the Pecos, Canadian, and Cimarron Rivers (Moore, 1944; Bottrell *et al*., 1964; Hatch *et al*., 1985; Lehtinen and Layzer, 1988; Taylor and Miller, 1990; Johnston and Page, 1992). No direct observations of broadcast spawning have been made *in situ* in these river systems (Moore, 1944; Bottrell *et al*., 1964). Studies using artificial eggs released in the river channel have shown that highly modified river reaches in the Rio Grande and Pecos River can transport BSM eggs great distances downstream (<30 to >150 km) (Dudley and Platania, 2007; Medley *et al*., 2007, 2009; Widmer *et al*., 2012). The magnitude of egg displacement is highly variable, dependent upon the complex interaction between discharge, channel dimensions, channel complexity, flow attenuation, channel storage, and river floodplain connectivity, but egg retention may be very efficient when coincident with ascending high flows and floodplain inundation. High rates of downstream egg drift and displacement observed in the contemporary Rio Grande are hypothesized to be a consequence of RGSM spawning in river reaches with severe habitat degradation that has created a ‘gun-barrel’ that ‘shoots’ eggs downstream, particularly in years when moderate to high flows are restricted to the main channel with few low-velocity habitats and little floodplain connectivity (Medley *et al*., 2007; Medley, 2009; Widmer *et al*., 2012).

EVIDENCE FOR FLOODPLAIN SPAWNING AND USE

Although we lack historical information on the use of backwater and floodplain habitats by RGSM larvae, in the contemporary Rio Grande, remaining floodplain habitats are used by larval fish and may provide more favourable conditions than the main channel (Pease *et al*., 2006; Magana, 2012). Recent studies have demonstrated that RGSM may preferentially spawn in backwaters and floodplain habitats when available (Fluder *et al*., 2007; SWCA Environmental Consulting, 2008, 2009, 2010, 2010, 2011; Gonzales *et al*., 2012). In May 2008, over 23 000 RGSM were captured using hoop nets set in natural and constructed shallow, low-velocity floodplain habitats, during a 3-week period coincident with spring runoff (SWCA Environmental Consulting, 2008, 2009). Many of these fish were gravid or showed signs of recent spawning, often expressing eggs when handled. Fluder *et al*. (2007) collected RGSM eggs primarily in inlets, inundated shelf habitats, and side channels in shallow habitats with dense grasses and sedges close to fish capture locations. Recent captures of gravid and spent RGSM entering seasonally flooded sites connected to the main channel during high flow years add credence to the minnow being a floodplain spawning fish (Table I) (SWCA Environmental Consulting, 2009, 2010, 2010, 2011; Gonzales *et al*., 2012).

On the basis of these observations, we suggest that RGSM enter and spawn in floodplain habitats with low-velocity flows or stationary water where eggs quickly settle after spawning, greatly enhancing egg retention rates. Broadcast spawning is successful in large lowland rivers as demonstrated by the historic distributions and life histories of the other *Hybognathus* species, five of which are found in small streams to large rivers within the Mississippi River drainage. For example, unpublished surveys of Missouri River habitat found *Hybognathus* larvae in floodplain scour pools that are continuously connected to the main channel, suggesting adults spawned in these environments (Galat *et al*., 2004; Whitledge *et al*., 2005). The reproductive strategy of broadcast spawning in floodplain habitat is also consistent with observations and original descriptions of other *Hybognathus* species observed spawning in pools and coves continuously connected to the main channel (Table II; Raney, 1939).

EVIDENCE OF AN UPSTREAM POPULATION MOVEMENT OR MIGRATION

Cross (1950) first provided anecdotal information suggesting the existence of a putative, short-distance spawning migration for BSM to explain observed changes in the abundance of plains minnows (*Hybognathus placitus*) in a tributary of the Cimarron River, Oklahoma. Two studies have attempted to directly document movement of BSM

Table I. Numbers of RGSM and RGSM eggs captured at habitat restoration sites in the Middle Rio Grande during spring monitoring (SWCA Environmental Consulting, 2009, 2010, 2010, 2011).

Year	Peak discharge in May[a]	RGSM captured in habitat restoration sites on floodplain	Relative percentage of fish community	RGSM eggs captured in floodplain habitat	RGSM eggs captured in main channel
2008	5150	2180	61·8	340	38
2009	4940	2057	81	23	85
2010	4900	403	56	112	300
2011	919[b]	39	5·8	0	6548[c]

RGSM, Rio Grande silvery minnow.

[a] At USGS Gage 08330000: Rio Grande at Albuquerque, NM.

[b] Almost all flow restricted to main channel and little floodplain inundation.

[c] Includes 3269 eggs caught in habitat restoration sites on margin of main channel due to lack of inundated floodplain habitat at low flows.

Table II. Habitat requirements and spawning ecology of seven species of *Hybognathus*.

Species	Spawning ecology
Hybognathus amarus (Rio Grande silvery minnow)	Spawn semi-buoyant, non-adhesive eggs in aquaria; eggs sank in aquaria if current not maintained (Platania and Altenbach, 1998; Cowley *et al*., 2009)
Hybognathus hankinsoni (brassy minnow)	Collected primarily from inlets and pools with little or no flow in the Des Moines River, Iowa; also collected from vegetated, sand-silt bottom pools in streams; adults spawn around peak flow (Starrett 1950; Starrett, 1951)
	Spawning took place in beds of vegetation in flooded lateral depressions, marshes, and ponds along a creek; eggs slightly adhesive to vegetation over a mud bottom (Copes, 1975)
	Adult brassy minnows moved to intermittent sloughs in the spring to spawn where young of year hatched and emigrated prior to summer drying; adults were observed in schools in permanent sloughs, but no reproduction was observed in permanent sloughs (Goldowitz and Whiles, 1999)
	Shallow and deep, large, vegetated backwater habitats; eggs adhesive to vegetation (Falke *et al.* 2010a,b)
Hybognathus placitus (plains minnow)	Spawn semi-buoyant eggs during high water in the Cimarron River; egg maturity correlated with increasing temperature; no direct spawning observed (Lehtinen and Layzer, 1988)
	Aggregated adults along sandbars and backwaters during receding flows; turbid water prevented observation of spawning (Taylor and Miller, 1990)
Hybognathus regius (eastern silvery minnow)	Spawning occurs in shallow (<0·3 m), quiet areas of backwater coves or lagoons near newly sprouted grass; non-adhesive, demersal eggs are scattered over debris on bottom of cove (Raney, 1939)
Hybognathus argyritis (western silvery); *Hybognathus hayi* (cypress minnow); *Hybognathus nuchalis* (Mississippi silvery minnow)	Unknown, but adults and larvae have been collected in backwater habitats

Girard (1856) collected *Hybognathus amarus* in a lagoon near Ft. Brown.

(Platania *et al*., 2003; Archdeacon and Remshardt, 2012) in the Rio Grande. Platania *et al.* released ~12 000 RGSM marked with visual implant elastomer tags. Sixty-six (66) recaptured fish showed that individual fish move long distances (ranging from 25·17 km upstream to 15·14 km downstream). However, net fish movement was ~257 m downstream. Similarly, Archdeacon and Remshardt (2012) released 6557 PIT-tagged RGSM and documented movement through a rock channel fishway to bypass a water diversion structure. Although both studies confirmed that small numbers of RGSM can swim long distances (Bestgen *et al*., 2010) and that a few RGSM may move upstream, both studies showed that RGSM also move downstream at a similar or greater magnitude, resulting in little net movement of the population. Neither study provided any evidence for a directed upstream population movement sufficient to overcome the observed and predicted egg displacement (30–150 km) in the contemporary Rio Grande (Dudley and Platania, 2007; Medley *et al*., 2007).

Reports summarizing two other unpublished datasets – the long-term RGSM population monitoring program data (Dudley and Platania, 2011) and the monitoring of visual implant elastomer-marked RGSM released to augment the wild RGSM population (Remshardt, 2008) – fail to document any evidence to support a hypothesized annual RGSM migration. Hoagstrom *et al*. (2008), in an analysis of long-term fish community monitoring data from the Pecos River, NM, also failed to provide any evidence of upstream migration of BSM, although migration has been presumed to occur. In summary, since Cross's initial presumption was published, we are unaware of any data or report, either peer-reviewed, published, unpublished, quantitative, or qualitative, that documents a population-scale, upstream movement or migration of the RGSM or any other BSM. Published papers supporting the theory offer only anecdotal or indirect evidence of migration and cite the growing number of previously published papers and unpublished theses and dissertations that rely on the original observations of Moore (1944) and the unconfirmed presumptions of Cross (1950) and others, to argue that long-distance upstream migration to overcome the observed magnitude of downstream egg displacement must be a fundamental aspect of these fishes' reproductive ecology (Platania and Altenbach, 1998; Luttrell *et al*., 1999; Bonner, 2000; Durham, 2000; Dudley and Platania, 2007; Hoagstrom *et al*., 2008; Perkin and Gido, 2011).

REINTERPRETATION OF RGSM REPRODUCTIVE ECOLOGY

Silvery minnows have been reported to be open-water, pelagic broadcast-spawning, non-guarding fish (sensu Balon, 1985), with semi-buoyant eggs that remain suspended to drift in turbulent flows (Platania and Altenbach, 1998). Such observations have led to the conclusion that the RGSM is a true pelagic spawning minnow and that eggs drift in the water column as a general strategy to avoid sedimentation and allow long distance, downstream dispersal (Platania, 1995; Platania and Altenbach, 1998; Bestgen *et al*., 2010). However, (1) the energetic utility of such a strategy for a small bodied fish has been questioned (Medley *et al*., 2007; Medley, 2009; Widmer *et al*., 2012), (2) the eggs lack oil globules or air vacuoles to aid drift (Figure 2), (3) the individual benefits and tradeoffs of such dispersal remain undefined and have not been quantified (PBS&J, 2011, report), and (4) recent monitoring suggests RGSM species enter available floodplain habitats to spawn during the rising limb of the spring snowmelt hydrograph (Gonzales *et al*., 2012).

Consequently, others have proposed that silvery minnows evolved a life history strategy that promotes egg retention and minimizes downstream population displacement and the need for upstream migrations (Raney, 1939; Medley *et al*., 2007; Medley, 2009; Widmer *et al*., 2012). Spawning in warm, seasonally flooded habitats with low flow, low-sediment concentrations, and high bed roughness (submerged vegetation) would allow newly expelled eggs to settle to the bed almost immediately where they would be efficiently retained. These warm habitats would allow eggs to hatch quickly, further reducing the potential for downstream egg displacement (Porter and Massong, 2006) and placing larvae and young of the year fish near excellent rearing habitat (Pease *et al*., 2006). Here, abundant food resources during floodplain inundation promote high growth rates, high juvenile survival, and greater recruitment into the adult population. The reported positive correlation ($r^2 = 0{\cdot}85$, $p = < 0{\cdot}0001$) between the magnitude of the total May and June flow at Albuquerque (Rio Grande at Albuquerque, USGS Gage 08330000) and October RGSM catch rates suggests that floodplain inundation during high flows is an important factor enhancing egg retention and promoting young of the year survival (Miller *et al*., 2008). Furthermore, fast, turbulent main channel flows are known to have severe negative impacts on drifting larval fish (Harvey, 1987).

Earlier reports of *Hybognathus* spawning ecology *in situ* suggested that they were demersal spawners, spawning over inundated floodplain vegetation in habitats connected to the main channel (Raney, 1939; Copes, 1975). More recent reports conclude that RGSM are pelagic spawners (Platania and Altenbach, 1998), although this was based on laboratory observations of spawning and eggs in aerated aquaria that made assumptions about spawning behaviour in the river environment. However, both conclusions may be relevant which suggests a complimentary interpretation of the observations. The ability of newly expelled eggs to settle quickly (Platania and Altenbach, 1998; Cowley *et al*., 2009) suggests that RGSM are primarily demersal spawners: *species that ascend off the bottom to release eggs that subsequently scatter and sink to the bottom*. Demersal spawning is consistent with our egg settling calculations, the lack of specific evolutionary adaptations that ensure eggs remain afloat, the original description of the fish, with laboratory observations of spawning (Platania and Altenbach, 1998; Cowley *et al*., 2009), with *in situ* observation of spawning habits of other *Hybognathus* species (Raney, 1939; Copes, 1975), with locations of *Hybognathus* larvae in floodplain habitats (Goldowitz and Whiles, 1999; Galat *et al*., 2004; Whitledge *et al*., 2005; Pease *et al*., 2006), and with recent observations in the Rio Grande that shows minnows use inundated floodplain habitats (Fluder *et al*., 2007; Gonzales *et al*., 2012). The high incidence of eggs reported in inundated floodplain vegetation in high flow years (Table I) also suggests that the species is an open substrate, non-guarding, phytophil, preferring to spawn over floodplain vegetation when available. Floodplain broadcast spawning is also consistent with historical accounts of available habitat in the Rio Grande floodplain (Crawford *et al*., 1993; Scurlock, 1998; Dean and Schmidt, 2011). Even though the RGSM lives in seasonally high-sediment environments, the species is still a member of a group of closely related BSM that has an ancestral commitment to demersal spawning (i.e. *Hybognathus*).

We propose that floodplain spawning and ontogenic changes in egg density likely evolved as an evolutionary stable strategy to promote egg retention and preferential settling in seasonally flooded warm, slow-moving, productive environments away from the relatively harsh conditions of the main channel and to prevent egg suffocation *subsequent* to egg settling. We suggest that change in egg density is a derived trait and the final density of water-hardened eggs is likely an evolutionary tradeoff between the reproductive benefits of egg settling and the costs of sediment-induced egg mortality

The available ecological information suggests that the current description of the reproductive life history of the RGSM be refined. Rather than an obligate main channel, pelagic spawning fish whose eggs drift long distances downstream, requiring a subsequent longitudinal upstream migration or long-distance dispersal of individuals, the available life history evidence suggests RGSM adults move laterally from the main channel to the floodplain to spawn in inundated floodplain vegetation or areas with little to no flow velocity (Fluder *et al*., 2007; SWCA Environmental Consulting, 2008, 2009, 2010, 2010, 2011). The evidence supports the conclusions of prior studies suggesting that spawning strategies and egg density of BSM evolved in response to a suite of selective pressures to maximize egg retention reduce the risks of sediment suffocation, promote young of year survival, and minimize downstream displacement of populations (Medley *et al*., 2007; Medley, 2009; Widmer *et al*., 2012). We suggest that the hydrodynamic mechanisms that promote egg retention and survival described in this paper may be generally applicable to other small bodied, broadcast-spawning fish species with drifting egg and larval stages living in large floodplain rivers.

To date, the evidence fails to support the presumption that upstream migration is a fundamental aspect of RGSM life history and BSM reproductive ecology. However, if upstream migration were confirmed, our hypothesis would not be invalidated. In the absence of a documented evolutionary benefit to long downstream dispersal, adaptive behaviours that employ passive mechanisms to reduce egg drift are energetically advantageous and will likely exist, even if some level of upstream migration is required to overcome an unavoidable level of downstream displacement (Speirs and Gurney, 2001).

CONSERVATION AND MANAGEMENT

Effective conservation and recovery of RGSM and other BSM populations requires an understanding of limiting factors. The difficulty identifying specific cause and effect relationships between the changes in fish communities and the environmental drivers that cause population declines is due to the multiple factors that might influence minnow populations, the complex management history, and the lack of high quality historic data.

Our review suggests that river fragmentation may not be the primary *cause* of the demise of the RGSM and other BSM (Dudley and Platania, 2007; Perkin and Gido, 2011). Rather, fragmentation is likely a general indicator, *correlated* to BSM extirpation that reflects the number of dams and the magnitude of numerous attendant geomorphic, hydrologic, and ecological impacts associated with their construction and use (Ligon *et al*., 1995). Water resource management changes the magnitude, frequency, duration, timing, variability, and rate of change of flows and often greatly reduces the total amount of water in the river, reducing the magnitude of large flows and increasing the frequency of low flows and river drying. Reservoir impoundment traps sediment and alters downstream thermal regimes (Robinson *et al*., 1998) and water quality. Changes in the relative balance of water and sediment fundamentally alter the natural geomorphology of these rivers (Lane, 1955). Sediment-starved river channels narrow, incise, and disconnect from their historic floodplains with a subsequent loss of habitat complexity and availability (Dean and Schmidt, 2011). These changes are promoted through tributary sediment control, river straightening and channelization, levee construction and river training using jetty jacks and non-native vegetation to improve flood control, increase channel stability and limit water conveyance losses (Scurlock, 1998; Cowley, 2006). These geomorphic changes altered the abundance and availability of both river channel and floodplain habitats and eliminated or changed the timing and magnitude of seasonal life history cues important for the reproductive ecology of these native fishes.

The physical effects of water resource development were greatly exacerbated by secondary biological management actions (Rinne and Miller, 2006). Native fish were poisoned to promote the establishment of non-native sport fisheries in the newly created cold-water habitats below hypolimnetic dam releases (U. S. Bureau of Sport Fisheries and Wildlife, 1962; Hubbs, 1963; Schmidt *et al*., 1998). Predatory sport fish were stocked in both the dam outlet and the reservoir impoundments where predation further impacted native fish. Additionally, the release of live bait has led to the establishment of closely related, non-native minnow species that have caused the extirpation and decrease of native minnow populations through competition and hybridization (Hoagstrom *et al*., 2010).

Removal of dams and irrigation diversions and the construction of fish passage have been proposed as the primary conservation and recovery strategy to address fragmentation (Dudley and Platania, 2007; Perkin and Gido, 2011). However, although longitudinal connectivity is a long-term genetics concern (Alò and Turner, 2005), in the absence of any data to indicate upstream fish migration there is little reason to believe that removal of irrigation diversion dams will be effective without improving habitat features that retain eggs and reduce drift (Speirs and Gurney, 2001). Authors of a recent independent evaluation of the feasibility of fish passage for RGSM at San Acacia Diversion Dam on the Rio Grande concluded that there is no evidence to suggest that RGSM migrate or that the provision of fish passage to re-establish longitudinal connectivity will benefit RGSM (PBS&J, 2011). They concluded that habitat restoration within reaches should be the highest priority. Additionally, removal of large mainstem dams and irrigation diversions is not a short-term feasible goal for managing endangered species, especially in the absence of evidence to support these actions.

Evidence supporting floodplain spawning coincident with rapidly increasing flows, and short egg drift distances in wide, geomorphically complex river reaches with connected floodplains (Medley *et al*., 2007; Gonzales *et al*., 2012; Widmer *et al*., 2012), suggests that restoration actions that promote historic channel geomorphology and river–floodplain connectivity in short river reaches is the near-term conservation need for demersal spawning BSM (Medley, 2009; PBS&J, 2011; Magana, 2012). Floodplain restoration will become more important in the future as vertical accretion of sediments during overbank flooding continues to reduce the areal extent of functional floodplain accessible to spawning fish. Management actions that restore the important natural attributes of the historic flow regime, remove bank stabilization structures such as jetty jacks, promote bank erosion and lateral migration of river channels, and create low-velocity main channel and floodplain habitat (pools, sloughs, and side channels) are likely to be beneficial (Gore and Shields, 1995; Sparks, 1995; MRGESACP (Middle Rio Grande Endangered Species Act Collaborative Program), 2004; Medley *et al*., 2007; Medley, 2009; Widmer *et al*., 2012).

In riverine environments where water use for habitat protection needs must be balanced by the increasing demand for other consumptive uses (agricultural, residential, and industrial), recovery activities must be based on science and clear understanding of cause and effect relationships. Although scientific uncertainty may remain, decisions must be made on the most parsimonious interpretation of the available evidence (Galat and Zweimüller, 2001). As once common species such as the RGSM become imperilled, scientists and river managers must place life history research in the context of historical conditions to understand the appropriate mechanisms to recover fish populations and restore fish habitat.

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