Ecological changes in aquatic communities in the Big Bend reach of the Rio Grande: Synthesis and future monitoring recommendations

Final Report submitted to Aimee Roberson, Desert Landscape Conservation Cooperative

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Cover:
Top, View of the Rio Grande oriented downstream from the overlook at Hoodoos river access point in Big Bend Ranch State Park (photograph by Brian Laub, USU)
Left, Embayment habitat in a sand bar in Boquillas Canyon, Bar 12 (photograph by Brian Laub, USU)
Center, Seining for fish in nearshore habitat in Boquillas Canyon, Bar 2 (photograph by Brian Laub, USU)
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Executive Summary

The Big Bend reach of the Rio Grande is an important region for binational collaboration on ecosystem management and restoration. The river is well protected from further development as a national wild and scenic river and by national and state parks on both sides of the border, but has been degraded over time primarily by altered hydrology, water quality degradation, and non-native species impacts. The success of future restoration and management efforts depend on a fuller understanding of the linkages between physical and chemical processes and biotic communities. A robust monitoring program in the region and targeted research are needed to supply this understanding. In this report, we synthesize information on the river ecosystem to describe changes to physical and biological properties and highlight key uncertainties in responses of biotic communities to dynamic physical and chemical conditions. We also provide recommendations for a monitoring program to address these uncertainties in the future and suggestions for targeted food web and fish research projects.

We reviewed existing literature relevant to the Big Bend region, including reports and published research conducted in the region and elsewhere on the Rio Grande. We also discussed ongoing research with local experts in the region, and solicited their opinion on important data gaps through an online survey. Current understanding of the river ecosystem was summarized in a conceptual model emphasizing links between physical, e.g., habitat and water quality, and biotic components, e.g., fish and invertebrate communities. Existing data on fish communities, active channel width, hydrology, and water quality at several sites were collected and analyzed using a structural equation model to gain insight into the relative importance of different controlling factors on the fish community and to demonstrate the potential utility of a coordinated research effort.

The historic flow regime of the river is characterized by several components including baseflows, Chihuahuan desert-derived flash floods, spring snowmelt floods, and channel resetting floods. Upstream dams and water use have altered the flow regime substantially, with overall declines in river flow volume and frequency and magnitude of large flood events. Spring snowmelt floods no longer occur, channel reset floods occur less frequently, and dam release flows from Mexico are now an important flow component. In alluvial reaches of the river, there has been persistent channel narrowing over time. During periods between reset flood events, sediment accumulates in the channel and floodplain, leading to channel narrowing. Historically, large magnitude flood events (> 1,000 m³/s) occurred with sufficient frequency to maintain a relatively wide channel, but reduced frequency of occurrence of reset floods has facilitated transition from a wide, shallow, multi-threaded system with an extensive low-elevation floodplain to a narrow single-thread channel with high banks. Channel narrowing has caused substantial habitat changes, including loss of shallow, slackwater habitats such as backwaters and submerged channel bars. Nonnative vegetation has exacerbated this process by promoting sediment deposition and stabilizing sediment deposits. The extent of channel narrowing has likely been less severe in canyon sections of the river, due to channel constriction and higher slopes. Water quality is poor above the Big Bend reach, upstream of the Rio Conchos confluence. Flow of the Rio Conchos, which supplies the majority of flow in the reach, improves water quality, and water quality steadily improves further through the Big Bend reach due to inputs of groundwater. Nonetheless, water quality has been degraded by reduced flow and upstream land use, with increases in salinity and nutrient levels over time, and periodic occurrence of low oxygen conditions. The changing flow, habitat, and water quality conditions have severely impacted biotic communities. Algal communities change substantially from
upstream to downstream through the reach, linked to changes in water quality and chemistry. Native mussels do not occur in the upstream sections of the reach, and only a few shells have been collected in the Lower Canyons section. Several native fish, including the federally listed Rio Grande silvery minnow, have been extirpated. Some non-native fish have colonized the reach, and abundance of remaining native fish has shifted to generalist habitat species tolerant of increased salinity.

One of the primary key uncertainties with regard to aquatic resources in the region revealed by the literature synthesis and supported by our expert opinion survey, is the relative influence of different limiting factors, including physical habitat, water quality, flood and drought events, and biotic interactions such as food limitations and competition and predation from non-native species. To address this and other uncertainties, our recommendation is to develop a suite of monitoring sites where efforts to measure these different limiting factors can be coordinated. If monitoring efforts are coordinated in this way, appropriate statistical methods can be used to integrate the data and understand the relative influence of different limiting factors. We demonstrate the use of one potential analysis, structural equation modeling, using existing data collected at several sites in the Big Bend region. The models suggest that active channel width, nonnative fish relative abundance, and hydrologic forcing all have strong direct effects on native fish species richness, and that water quality and hydrologic forcing have strong indirect effects on native species richness through nonnative relative abundance. The models also reveal that primary limiting factors differ for different fish species; for example, water quality had strong direct effects on river carpsucker relative abundance, but relatively weak direct effects on relative abundance of Tamaulipas shiner or red shiner. Although data limitations make the conclusions preliminary, the models provide an example of how data collected under a coordinated monitoring campaign can be analyzed.

We also develop a series of hypotheses and recommendations for studies investigating the major limiting factors for reestablishment of Rio Grande silvery minnow. The two main hypotheses are that Rio Grande silvery minnow are present but not detected, or that they are not surviving or reproducing in the wild. To address the former hypothesis, we recommend mounting a high-intensive monitoring trip across a large spatial extent. If Rio Grande silvery minnow are indeed at low abundance, several potential hypotheses for explaining their low abundance can be investigated, and we provide recommended study approaches for doing so. These hypotheses include potentially poor adaptation of stocked fish to local conditions, lack of available physical habitat, and an alternative food web state compared to historic conditions.

Substantial effort has been expended to gain the current understanding of the Rio Grande in Big Bend. Future efforts to coordinate monitoring can build on this understanding to help guide management and restoration of aquatic resources. Developing these coordinated efforts will be critical over the next several decades, to help guide binational collaboration under changing climate and increased pressure on water resources.
The Rio Grande/Río Bravo in the Big Bend region is a vital river for aquatic species conservation. The Big Bend region (between the Rio Conchos confluence and Amistad Reservoir/Pecos River confluence) harbors a relatively intact native fish community (Heard et al. 2012) and has been designated as a reintroduction site for the endangered Rio Grande silvery minnow (USFWS 2008a). The integrity of the invertebrate community also appears high in the region. All recently sampled sites rate as intermediate to exceptional based on macroinvertebrate aquatic life use indices (Diaz and Araujo 2013, Diaz et al. 2014), and the region likely supports populations of sensitive mussel species at least in downstream reaches (URGBBEST 2012). The river is free-flowing through the Big Bend reach, with relatively little water use compared to neighboring river segments (Brock et al. 2001), and has been designated as a wild and scenic river from the Chihuahua/Coahuila state border to the Terrell/Val Verde County (Texas) border (NPS 2004). Much of the surrounding land along the river is managed in national and state parks and natural reserve areas (URGBBEST 2012). The importance of the region has been recognized by both Mexico and the United States, who are working together to designate the area as a natural area of binational interest (Obama and Calderón 2010). With this report, we aim to contribute to conservation efforts in the region by identifying critical scientific data gaps regarding aquatic biota and recommending study approaches to address them.

Although the river is free-flowing through the reach, the hydrology has been substantially altered from historic conditions by upstream dams and water use, as well as a general decreasing trend in precipitation (Everitt 1993, Schmidt et al. 2003, Porter et al. 2009, Sandoval-Solis et al. 2010, Miyazono et al. 2015). Nearly all of the water flowing through the Rio Grande mainstem is used for agricultural, industrial, and municipal purposes in the states of Colorado, New Mexico, Texas, and Chihuahua, Mexico. Currently, the Rio Conchos, whose watershed is located entirely within Mexico, supplies the majority of the flow entering the Big Bend region (Miyamoto et al. 1995). Altered flow conditions, in combination with non-native vegetation encroachment, have led to substantial changes in channel morphology, with persistent channel narrowing and loss of channel complexity over the last 100 years (Everitt 1993, Dean and Schmidt 2011, Garrett and Edwards 2014), interrupted only occasionally by large magnitude flood events that temporarily rewidened the channel (Dean and Schmidt 2013). The changing flow and habitat conditions, combined with establishment of non-native fish and degradation of water quality, have impacted the native aquatic biota, with the silvery minnow and a few other species having been extirpated and many other native fish currently persisting in lower abundance than historically (Treviño Robinson 1959, Hubbs et al. 1977, Bestgen and Platania 1991, Platania 1991, Anderson et al. 1995, Edwards et al. 2002, Edwards 2005, Hoagstrom et al. 2010a, Winemiller et al. 2010, Karatayev et al. 2012, URGBBEST 2012, Garrett and Edwards 2014, Miyazono et al. 2015).

Thus, despite the free-flowing and relatively well-protected state of the Rio Grande in the Big Bend region, substantial management and restoration efforts are being conducted and considered to ensure the persistence of native aquatic biota in the region. These efforts include habitat improvement projects, primarily non-native vegetation removal in selected areas (Schmidt and Dean 2011), reintroduction of the endangered Rio Grande silvery minnow (USFWS 2008b), and development of managed flow recommendations (Sandoval-Solis and McKinney 2014). Efforts to develop flow recommendations are in the early stages, and include exploration of relevant legal frameworks (Brock et al. 2001), modelling to determine feasibility and tradeoffs of different environmental flow scenarios...
(Sandoval-Solis and McKinney 2009), and review of scientific considerations for environmental flows (URGBBEST 2012, Sandoval-Solis and McKinney 2014). Research by state, federal, and university personnel has provided important insights into the distribution, organization, and changes in aquatic communities in the region over time (see review below), and has provided critical guidance for ongoing river management efforts. However, the increasing focus on rehabilitation of the river ecosystem in the Big Bend region, including possible development of an ecological flow program, has highlighted the need for continued scientific investigations under a coordinated plan, in order to address key research gaps and help guide river management (Schmidt and Dean 2011, URGBBEST 2012).

To achieve our goal of identifying gaps in understanding of the aquatic biota in the region, we provide a review of the existing scientific understanding of the river system. We synthesize the current understanding in a conceptual model of the river that emphasizes linkages between hydrologic, geomorphic, and ecological components. Based on the model, we highlight uncertain or unknown relationships between the different components that can be used as research questions for future scientific investigations, and solicit expert knowledge on which of these questions are most critical to answer over the next 5-10 years. Using expert opinion as guidance, we propose a general framework for future monitoring efforts on the river, and provide an example analytical approach that could be used to integrate disparate data sources collected under the proposed monitoring framework. We also develop a set of research hypotheses and approaches for investigating the issue of the current limited success of Rio Grande silvery minnow reintroduction efforts.

**Literature Review and Synthesis**

**Conceptual Models**

Based on the available literature and input from local experts, we developed a general conceptual model of the river system emphasizing linkages between hydrologic, geomorphic, and ecological components (Figure 1). In talking with experts, it was clear that a single detailed model for the entire Big Bend reach would not adequately capture the variation in river channel morphology and associated geomorphic and hydrologic processes that structure aquatic communities. Instead, we developed two detailed conceptual models, one for the more alluvial floodplain-dominated sections of the reach (most of the river from the Rio Conchos confluence to La Linda, but excluding canyon sections; hereafter the alluvial reach; Figure 2), and one for the canyon-bound sections of the reach (primarily the Lower Canyons section downstream of La Linda; hereafter the Lower Canyons reach; Figure 3). Much more information regarding channel response to hydrologic forcing events, primarily floods and extended droughts, is available for the alluvial reach than the Lower Canyons reach, and it is likely, though uncertain that channel morphology and aquatic communities will respond differently to hydrologic forcing events in the Lower Canyons reach (Schmidt and Dean 2011, URGBBEST 2012). In the following sections we step through the components and linkages of these models as informed by research conducted in the Big Bend region and throughout the Rio Grande Basin.
Figure 1. Overall conceptual model of the Rio Grande ecosystem in the Big Bend region. Boxes indicate physical or biological components, circles indicate important processes, and arrows indicate direction of influence. Colors correspond to different major components including hydrology (blue), geomorphology (brown), vegetation (green), habitat (orange), and aquatic biota (gold). See figures 2 and 3 for more detailed models for the alluvial reach and Lower Canyons reach, respectively.
Figure 2. Detailed conceptual model for the alluvial floodplain reach of the Rio Grande excluding canyon sections. Model has similar structure as the overall model in figure 1, except that black arrows indicate negative relationships, i.e., an increase in the driving variable causes a reduction or decrease in the response variable, red arrows indicate positive relationships, and blue arrows indicate neutral responses. Unknown or uncertain relationships are highlighted by dashed arrows.
**Figure 3.** Detailed conceptual model for the Lower Canyons reach of the Rio Grande. See description under figure 1 and 2 for interpretation of model components.
Hydrologic Components

In their environmental flow recommendations report for the Upper Rio Grande basin in Texas, URGBBEST (2012) identified five important flow components for the Rio Grande in Big Bend: subsistence flows, baseflows, dam release flows, flash floods, and channel resetting floods. In the model, we conceptualize subsistence flows as being very low baseflows, and model decreases in baseflow as having negative impacts on water quality (Figures 2 and 3). We also discuss the role of spring snowmelt-driven floods in the Big Bend region, but otherwise follow the URGBBEST (2012) definitions in discussing the historic flow regime.

Baseflows

Baseflows are flows that persist during periods without precipitation, and are maintained primarily by upstream inflows in the upper alluvial reaches and primarily by groundwater and spring inputs in the Lower Canyons (URGBBEST 2012). The section of river immediately downstream from the Rio Conchos confluence is a losing reach, primarily caused by agricultural withdrawals, but baseflow magnitude tends to increase through the Big Bend National Park and Lower Canyons section because of cumulative inputs from natural groundwater seeps and springs (Porter et al. 2009, Bennett 2011, Raines et al. 2012, Miyazono et al. 2015).

Chihuahuan Desert-derived flash floods

Flood events are geomorphically-important flows, with often more than 90% of annual suspended sediment load transported during a few flood events (Horowitz et al. 2001). Flash floods are spikes in flow magnitude of short duration and localized extent, derived from thunderstorm-generated rainfall events in ephemeral tributaries.

Spring snowmelt floods

Spring floods were historically derived from snowmelt runoff in the Rocky Mountain headwaters of the Rio Grande. These floods are known to be important for reproduction and life history timing of many native fish in the middle Rio Grande in New Mexico, but some species spawn during low-flow periods in the middle Rio Grande (Pease et al. 2006), and the geomorphic and ecological importance of spring floods is less well known in the Big Bend region. The natural hydrology of the Big Bend region of the Rio Grande is substantially different from upstream regions, with peak discharge typically occurring during September, as opposed to the spring, due to the influence of the Rio Conchos, whose hydrology is determined by rainfall patterns rather than snowmelt (Schmidt et al. 2003, Sandoval-Solis et al. 2010). Nonetheless, there was certainly a rise in flow during the late spring even below the Rio Conchos (see Figure 3 in Schmidt et al. 2003), and there has been little opportunity to study their impact, because water development in the Rio Grande basin has been ongoing for as long as flow gages have been operating on the Rio Grande in the Big Bend region (Schmidt et al. 2003). Thus, spring floods may have been an important component of the historical hydrograph, but their importance relative to other hydrological components is uncertain.

Channel resetting floods

Channel resetting floods have been defined as large-magnitude (> 1000 m$^3$/s), long-duration floods that, at least in the alluvial reach, counteract channel narrowing and rewidens the river channel (Dean and Schmidt 2011). Reset floods rewidens the channel by stripping vegetation from the floodplain and eroding, transporting, and depositing large quantities of sediment through the river channel (Dean...
Currently, reset floods arise from precipitation associated with dissipating tropical depressions falling primarily in the Rio Conchos Basin, though spring snowmelt floods may have historically reached reset flood level discharges (Dean and Schmidt 2011). Historically, these floods likely occurred frequently enough to prevent channel narrowing, but since the 1940s, only five reset-level floods have occurred, and have only temporarily reset a persistently narrow channel (Dean and Schmidt 2011).

**Dam release flows**

Water development in both the United States and Mexico has substantially altered the flow regime in the Big Bend region (Kelly 2001, Schmidt et al. 2003, Porter et al. 2009, Sandoval-Solis et al. 2010, Gutiérrez and Johnson 2014, Miyazono et al. 2015). As mentioned above, Rocky Mountain derived spring snowmelt floods have been eliminated. In addition, water use upstream in the Rio Grande has nearly eliminated incoming Rio Grande flow to the reach. Instead, nearly all flow at the upstream end of the reach is contributed by the Rio Conchos (Miyamoto et al. 1995, Edwards 2005, Porter et al. 2009). Flows entering the Rio Grande from the Rio Conchos are controlled by releases from Luis Leon Dam in Mexico, and these dam release flows are now another important component of the flow regime in the region (URGBBEST 2012).

**Water quality issues**


Despite the generally improving water quality through the length of the reach, water quality has generally been declining over time as flow levels in the Rio Grande and Rio Conchos have been declining over the last several decades (Miyamoto et al. 1995, Contreras-Balderas et al. 2002, Porter et al. 2009, Gutiérrez and Johnson 2014, Miyazono et al. 2015). The river is listed as impaired by the Texas Commission on Environmental Quality due to not meeting standards for chloride, sulfate, and total dissolved solids (TCEQ 2014). Continuous monitoring of oxygen concentration at several flow gages has shown that brief periods of hypoxia (low oxygen conditions) occur periodically (Figure 4). Concentrations of some contaminants such as DDT and PCBs have been declining through time due to discontinued use (Lee and Wilson 1997, Van Metre et al. 1997, Edwards 2005, Schmitt et al. 2005), but some pesticides and other dissolved organic compounds are still found at detectable levels in water and
sediment samples in the river (Lee and Wilson 1997, Van Metre et al. 1997, Moring 1999, Schmitt et al. 2005). Historic mining in the region still poses a threat to water quality, because levels of metals such as mercury are elevated in soils near abandoned mine sites (Gray et al. 2006). Although delivery of these metals to the Rio Grande is infrequent due to the dry climate (Gray et al. 2006), and levels are generally near background amounts (Porter et al. 2009), atmospheric deposition can also bring contaminants such as mercury into the river system (Lee and Wilson 1997, Van Metre et al. 1997, Lambert et al. 2008), and select samples have indicated potentially problematic levels in surface water, streambed and Luis Leon Reservoir sediments, and fish tissue (Miyamoto et al. 1995, Lee and Wilson 1997, Van Metre et al. 1997, Schmitt et al. 2005, Lambert et al. 2008, Gutiérrez 2000, Smith et al. 2010).

![Figure 4](image-url)  
*Figure 4. Discharge (blue) and dissolved oxygen concentration (green) at USGS Rio Grande Village flow gage (#08375300). Note several occurrences where dissolved oxygen drops below 2 mg/L, indicating brief occurrence of hypoxia.*
Channel Geomorphic Components

Channel morphology of the Rio Grande has changed significantly over the last 100 years due primarily to increasing alteration of the river flow regime (Everitt 1993, Schmidt et al. 2003, Porter et al. 2009, Dean and Schmidt 2011, Swanson et al. 2011). In the alluvial reach in particular, the channel was historically wide, shallow, and multi-threaded with an extensive floodplain that was low in elevation relative to the river channel (Everitt 1993, Schmidt et al. 2003, Porter et al. 2009, Dean and Schmidt 2011). Tributaries supply coarse and fine sediment, which was historically frequently mobilized by flood activity (Everitt 1993, Dean and Schmidt 2011, Dean et al. 2016), likely forming and maintaining gravel bars and other complex sediment deposits. The width of the Lower Canyons reach is necessarily constricted by bedrock canyon walls, but was nevertheless likely wider historically than in recent decades (Dave Dean, personal communication).

The wide, multi-thread historic channel likely provided a variety of complex habitats used by native aquatic organisms. In particular, shallow, slow-velocity habitats such as embayments, backwaters, and floodplain pools, which are often favored by young life stages of fish due to their favorable temperatures and high productivity (Schlosser 1991, Dudley and Platania 1997, Pease et al. 2006), were likely abundant. Submerged gravel bars were also likely prevalent. Where the river encountered bedrock and large boulders, cracks in the rock and substrate-boulder interfaces, favored by some species of freshwater mussels, such as the Texas hornshell (*Popenaias popeii*) (Karatayev et al. 2012, Inoue et al. 2014) were likely more available.

The channel has narrowed appreciably over the past 100 or so years, and especially over the last 70 years (Everitt 1993, Schmidt et al. 2003, Dean and Schmidt 2011). Today, the channel is characterized by a small width:depth ratio and a floodplain standing relatively high above the single-thread channel (Everitt 1993, Dean and Schmidt 2011). Many gravel bars and off-channel habitats have been filled with fine sediment (Dean et al. 2011, URGBBEST 2012), and sediment brought in by flow events in ephemeral tributaries is infrequently mobilized, leading to build-up of sediment in the channel and a stair-stepped longitudinal profile, with substantial elevation drops at tributary junctions (Everitt 1993, Dean and Schmidt 2013). Narrowing has been less prevalent in the Lower Canyons section due to the natural constriction on historic channel width, but has still occurred to some degree in this reach.

Physical Habitat

Narrowing of the channel likely reduced the availability of complex physical habitats, particularly the shallow slow water habitats, due to infilling with sediment (URGBBEST 2012). Loss of complex habitat through channel narrowing has been observed in other desert rivers, and similarly to the Rio Grande, has prompted efforts to restore channel habitat in order to conserve native fish (Laub et al. 2015). Fine sediment deposition has also likely reduced the availability of submerged gravel bars and may have even impacted bedrock and large boulder habitat (Inoue et al. 2014), though the extent of impacts to bedrock habitat is not well known. The most common available habitat in the current alluvial areas is sandy run habitat, though the availability of fast-water habitat over coarse substrate increases in canyon sections and may also have increased around tributary junctions (Davis 1980, Moring 2002, Edwards 2005, Dean and Schmidt 2013, Garrett and Edwards 2014).
Vegetation Components

Although little is known about historic vegetation structure in the reach prior to extensive water development, native vegetation likely persisted in relatively isolated and low density stands due to the wide active channel and frequent bed mobilization (URGBBEST 2012). Floodplain vegetation included stands of willow (Salix spp.), mesquite (Prosopis spp.), and grasses and other woody plants, with stands of cottonwoods (Populus fremontii) occurring in the upstream portions of the reach (Engel-Wilson and Ohmart 1978, URGBBEST 2012). Currently, patches of native vegetation still persist, but filling in of the active channel and less frequent sediment mobilization has allowed non-native vegetation, primarily salt cedar (Tamarix spp.) and giant cane (Arundo donax), to colonize the river corridor in dense stands (Engel-Wilson and Ohmart 1978, Everitt 1998, Porter et al. 2009, Dean and Schmidt 2011, URGBBEST 2012, Garrett and Edwards 2014).

Aquatic Communities

Mussels

Freshwater mussels are one of the most imperiled groups of organisms in North America, with 70% listed as threatened, endangered, or of special concern two decades ago (Williams et al. 1993). The Rio Grande in Texas hosts a unique assemblage of mussel species (Winemiller et al. 2010, Burlakova et al. 2011a, 2011b, Karatayev et al. 2012), because it is located in a transition zone between the Central American mussel fauna and the Gulf of Mexico-Mississippi River Basin fauna (Haag 2010). Although little is known about the historic mussel assemblage in the Big Bend region (Winemiller et al. 2010), it is likely to be an important area for conservation of native Rio Grande mussels, due to its protection in a free-flowing state and its relatively intact assemblage of native fish, which mussels use as hosts and for dispersal during the larval stage. Populations of the salina mucket (Potamilus metnecktayi), Mexican fawnsfoot (Truncilla cognata), and Texas hornshell have been found in the Rio Grande below Amistad Reservoir (Karatayev et al. 2012), and several shells of Texas hornshell and salina mucket have been found in the Big Bend reach (Howells 2004), suggesting that the Big Bend reach may currently support additional populations of these species, or could serve as a site for establishment of new populations, which is urgently needed for many species to ensure long-term viability (Haag and Williams 2014).

Native fish

The Big Bend region still supports most of the native fish species thought to occur historically, but several species have been or are nearly extirpated including the Rio Grande silvery minnow, Rio Grande blunt-nose shiner (Notropis simus simus), shovelnose sturgeon (Scaphirhynchus platorynchus), and Rio Grande shiner (Notropis jemezanus) (the Rio Grande silvery minnow has subsequently been reintroduced) (Hubbs 1958, Hubbs et al. 1977, Hubbs et al. 2008, Heard et al. 2012, Garrett and Edwards 2014). Non-native fish, including common carp (Cyprinus carpio), plains killifish (Fundulus zebrinus), and inland silverside (Menidia beryllina) have colonized the reach, but the Big Bend region still supports a greater proportion of native than non-native species (Heard et al. 2012). The relative abundance of native species, however, has been changing in recent decades (Edwards et al. 2002, Garrett and Edwards 2014, Miyazono et al. 2015). Blue sucker (Cycleptus elongatus), speckled chub (Macrhybopsis aestivalis), and longnose dace (Rhinichthys cataractae) have declined, whereas red shiner (Cyprinella lutrensis), mosquitofish (Gambusia affinis), and Tamaulipas shiner (Notropis braytoni) have been
increasing in abundance. As part of the recovery plan for Rio Grande silvery minnow, reintroduction efforts have been ongoing in the reach since 2008 (see reintroduction timeline in Table 1). There is some indication that these efforts could be successful, based on the observation of Rio Grande silvery minnow eggs in the reach in 2010 and the last several years (Edwards and Garrett 2013, Aimee Roberson, personal comm.); however, recruitment is likely limited due to the low observed abundances of age-1 fish (Edwards and Garrett 2013). In our recommendations sections below, we outline a research program that could be used to systematically investigate the critical issue of limitations to success of Rio Grande silvery minnow reintroduction efforts.

**Table 1. Important dates in the Rio Grande silvery minnow reintroduction effort in the Big Bend region.** Numbers of stocked fish, stocking locations, and hatchery used are provided for each stocking event. Information from M. Montagne (USFWS, personal communication), Edwards and Garrett (2013), Southwestern Native Aquatic Resources & Recovery Center (SNARRC) newsletters (December 2014, November 2015), and USFWS Open Spaces blog from October 20, 2015 ([http://www.fws.gov/news/blog/index.cfm/2015/10/20/Native-Texans-Rio-Grande-Silvery-Minnows-from-Texas-Stocked-in-Big-Bend-National-Park](http://www.fws.gov/news/blog/index.cfm/2015/10/20/Native-Texans-Rio-Grande-Silvery-Minnows-from-Texas-Stocked-in-Big-Bend-National-Park)).

<table>
<thead>
<tr>
<th>Date</th>
<th>Event</th>
<th>Number Stocked</th>
<th>Stocking Locations</th>
<th>Hatchery Used</th>
</tr>
</thead>
<tbody>
<tr>
<td>~1960</td>
<td>Extirpated from Big Bend reach</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>July 20, 1994</td>
<td>Listed as federally endangered</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>July 8, 1999</td>
<td>Recovery plan finalized</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>December 2008</td>
<td>Reintroduction plan approved</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>December 2008</td>
<td>First reintroductions</td>
<td>431,000 (250,000 age-0, 150,000 age-1)</td>
<td>Grassly Banks, Terlingua Creek Mouth, Rio Grande Village, Adams Ranch</td>
<td>SNARRC (Dexter National Hatchery)</td>
</tr>
<tr>
<td>October 2009</td>
<td>Stocking</td>
<td>~510,000</td>
<td>Same as above</td>
<td>SNARRC</td>
</tr>
<tr>
<td>October 2010</td>
<td>Stocking</td>
<td>500,000</td>
<td>Same as above</td>
<td>SNARRC</td>
</tr>
<tr>
<td>October 2011</td>
<td>Stocking</td>
<td>~300,000</td>
<td>Same as above</td>
<td>SNARRC</td>
</tr>
<tr>
<td>October 2012</td>
<td>Stocking</td>
<td>120,000</td>
<td>Same as above</td>
<td>SNARRC</td>
</tr>
<tr>
<td>October 2013</td>
<td>Stocking</td>
<td>72,000</td>
<td>Dryden (Shaffer’s Crossing)</td>
<td></td>
</tr>
<tr>
<td>December 2014</td>
<td>Stocking</td>
<td>70,000</td>
<td>Dryden (Shaffer’s Crossing)</td>
<td>SNARRC</td>
</tr>
<tr>
<td>October 2015</td>
<td>Stocking</td>
<td>239,000</td>
<td>227,000 at Dryden (Shaffer’s Crossing) 2,000 at Terlingua Abajo</td>
<td>132,500 from Uvalde National Fish Hatchery (Texas) 94,500 from SNARRC</td>
</tr>
<tr>
<td>November 2015</td>
<td>Stocking</td>
<td>83,618</td>
<td>Dryden (Shaffer’s Crossing)</td>
<td>SNARRC</td>
</tr>
</tbody>
</table>
Hydrologic-Geomorphic Linkages

As mentioned above, most of the research on Rio Grande geomorphology has been conducted in the alluvial floodplain reach of the river, with little information collected in the Lower Canyons. Thus, the following discussion applies primarily to the alluvial floodplain reach.

The timing and magnitude of hydrologic forcing events has been the primary control on the geomorphic organization and changes in channel morphology on the Rio Grande in the Big Bend region. The river has been characterized as a disequilibrium system (Dean and Schmidt 2013). Over the past 100 years, the channel has undergone periods of channel narrowing, periodically interrupted by large magnitude reset floods that rewidен the channel (see figure 17 in Dean and Schmidt 2011). Narrowing is induced during periods of low flow in between reset floods by the accumulation of sediment on the river floodplain and within the channel (Everitt 1993, Dean and Schmidt 2011, Dean et al. 2011). The majority of deposited sediment is provided by ephemeral tributaries that regularly produce short duration, high sediment load flood events during the summer and fall (Everitt 1993, Dean et al. 2011, Dean et al. 2016). These tributary-derived flood events attenuate quickly in the Rio Grande mainstem, and most of the sediment and organic matter is deposited in downstream reaches of the mainstem (Everitt 1993, Dean et al. 2011, Dean et al. 2016). Moderate magnitude flows, such as those provided by dam releases on the Rio Conchos, transport small incoming sediment loads compared to floods from ephemeral tributaries (Dean et al. 2011), and can thus mobilize and transport fine sediment through the reach; whether large-scale erosion or deposition occurs within the Rio Grande is dependent on existing sediment supply within the channel and the magnitude and duration of flood flows (Dean et al. 2016). Coarse sediment also accumulates at tributary junctions during periods between large flood events (Dean and Schmidt 2013), and this sediment accumulation creates a stair-stepped longitudinal profile by ponding water upstream from these junctions (Everitt 1993). Moderate dam release flows can erode gravel at tributary junctions and thus help maintain a smoother longitudinal profile (D. Dean, USGS, personal communication). Some narrowing, particularly around tributary junctions, can be prevented when meander cutoffs form, temporarily increasing channel gradient and providing enough flow energy to prevent further bed deposition (Everitt 1993, Schmidt et al. 2003). However, large-scale rewidening only occurs during reset floods, which have sufficient magnitude and duration to erode and transport sediment through the reach, rewidening the channel, grading the longitudinal profile, creating in-channel gravel bars, and depositing sediment on the floodplain (Dean and Schmidt 2013). The most recent reset floods have been generated in the Rio Conchos Basin by dissipating tropical storms (Dean and Schmidt 2013). Historically, spring snowmelt generated by runoff from the Rocky Mountains in Colorado and New Mexico likely also caused erosion, but the relative importance of spring snowmelt floods is uncertain, as they have been eliminated in the region due to water development projects upstream.

When reset floods occur, the greatest degree of channel change is observed at tributary junctions, where the river is most sinuous, and at grade controls and width constrictions provided by bedrock forcing (Dean and Schmidt 2013). The river widens substantially downstream of tributary inputs, because the coarse sediment accumulated at tributary inputs is mobilized by the flood and generates large spatial velocity gradients that work to scour vegetation and erode channel banks. The river also has higher energy at tributary junctions and at bedrock grade controls, due to the elevated slope. A similar phenomena occurs at bedrock width constrictions, as the narrowing of the channel
forces an increased flow velocity. Channel sinuosity aids channel widening by creating high-energy turbulent eddies that have the capacity to erode sediment and scour vegetation.

**Vegetation Feedbacks on Channel Geomorphology**

Floodplain vegetation, particularly non-native tamarisk and giant cane, exert a feedback influence on channel narrowing in the Big Bend region (Dean and Schmidt 2011). During extended periods of low flows, non-native vegetation can colonize deposited sediment in thick stands and stabilize banks and floodplain sediments, further exacerbating narrowing by preventing sediment mobilization during moderate flood events and increasing deposition by slowing flow velocities (Engel-Wilson and Ohmart 1978, Dean et al. 2011). Channel narrowing reduces channel capacity, allowing smaller floods to escape the channel, thereby depositing additional sediment on the floodplain, and creating a positive feedback mechanism (Everitt 1993, Everitt 1998, Dean and Schmidt 2011, Dean et al. 2011). Reset floods have sufficient power to erode sediment and scour vegetation (Dean and Schmidt 2013), and these floods may promote native vegetation persistence by removing non-native vegetation and creating bare alluvial surfaces for colonization.

**Geomorphic-Physcial Habitat Linkages**

The changing geomorphic organization of the river channel and floodplain alters the available physical habitat for aquatic organisms in the region. Each species has a particular set of habitat requirements, and it is unlikely that preferred habitat for all species will be maximized at a particular state of channel morphology (Laub and Budy 2015). However, there is a general ecological principle that greater habitat heterogeneity, i.e., a greater diversity of habitats, will support a greater number of species (Ricklefs and Schluter 1993), and support for this principle has been found on the Rio Grande (Davis 1980, Platania 1991, Heard et al. 2012). Thus, a more complex channel morphology is more likely to provide needed habitat for more species than a simplified channel morphology. An important question is how has the complexity of the channel changed with changes in geomorphic organization over time?

The working model is that after reset floods widen the channel and redistribute sediment into gravel bars, the complexity of the channel is increased, and over time, as the channel narrows, complexity decreases as particular habitat types are lost. Available data on the Rio Grande in the alluvial reach supports this model (Box 1). Shallow, slow-velocity habitats such as backwaters, floodplain pools, embayments, and shallow edges are less prevalent during times when the channel is narrow, because these habitats are filled in by sediment deposition (URGBBEST 2012, Garrett and Edwards 2014). These types of habitat are important for many of the species of greatest management focus in the Big Bend region (Garrett and Edwards 2014, Moring et al. 2014). Some types of habitat increase in prevalence as the channel narrows, including sandy run habitat and large-substrate dominated riffles, the latter being prevalent at tributary junctions (Dean and Schmidt 2013, Garrett and Edwards 2014). However, armoring of riffles and rapids by coarse sediment can degrade the quality of these habitats (URGBBEST 2012). Furthermore, coarse-grained riffles and sandy runs are present after reset floods, such that the overall effect of channel narrowing is likely a reduction in channel complexity and habitat diversity (Dean and Schmidt 2011, URGBBEST 2012, Garrett and Edwards 2014; Box1).
The relationship between channel width and channel complexity is less certain in the Lower Canyons reach. Channel width does vary in this reach and narrowing likely eliminates backwaters and other slow velocity habitats in this reach as well (Garrett and Edwards 2014), but the magnitude of channel narrowing and associated habitat impacts is likely lower in the canyon sections. The Lower Canyons reach is more frequently dominated by bedrock and cobble bed substrate, and width is constricted by bedrock canyon walls, as opposed to the generally more shallow, sandy braided alluvial reaches (Edwards 2005), and these differences may make reductions in width less important in terms of reducing available habitats in the Lower Canyons, compared to the alluvial reach. In addition, the trajectory of habitat changes during channel narrowing is unknown. There may be a linear relationship between channel width and habitat complexity, or there may be a threshold pattern, wherein narrowing below a certain point dramatically reduces habitat diversity. The trajectory of change has important management implications, because in the former case, management would want to maintain the channel as wide as possible, whereas in the latter case, maintaining the threshold width is essentially as good as maintaining a channel twice or ten times as wide. Although a linear trend is plotted on the graph of available data (Box 1, Figures 5 and 6), the range of widths is too narrow and number of data points too low to say for certain that a linear trend will hold across a broader range of channel widths.

**Box 1.** Relationship between active channel width and habitat diversity.

Available research on the Rio Grande in the alluvial reach supports a positive relationship between channel width and diversity of available habitats (Figures 5 and 6). We compiled habitat data from Heard et al. 2012 and Moring et al. 2014 with channel width data from Dean and Schmidt 2013 to explore whether the number of mesohabitats and mesohabitat richness increased with channel width following the 2008 reset flood, as expected. Habitat data from Heard et al. 2012 and Moring et al. 2014 were not collected with the same methods, so we modified the data of each to make them more comparable. Heard et al. 2012 sampled habitat and fish monthly at seven sites in the Big Bend reach in 2006. We used data from five of these sites — Santa Elena (Terlingua Creek mouth), the gage at Johnson Ranch, Johnson Ranch, Hot Springs (Tornillo Creek mouth), and upstream of Boquillas canyon. Heard et al. 2012 identified pool, run, riffle, eddy, side channel, and backwater mesohabitats during transect-based fish sampling. Heard et al. 2012 did not focus specifically on mapping mesohabitats, and the data obtained reported a series of seine hauls moving from downstream to upstream and across a series of transects. We tallied the number of mesohabitats by counting a new mesohabitat every time a new seine haul was reported as occurring in a different mesohabitat than the previous seine haul.

Moring et al. 2014 mapped mesohabitats at three sites in the Big Bend region in 2010 and 2011 at three different flow levels, which they identified as high, intermediate, and low. We used data from two of their sites — Santa Elena (Terlingua Creek mouth) and Rio Grande Village. Moring et al. 2014 also mapped pool, run, riffle, and backwater habitats, but also mapped forewaters, embayments, rapids, and submerged channel bars. We reduced the number and richness of mesohabitats in the Moring et al. 2014 data for each sampling reach and flow level by excluding submerged channel bars,
assuming rapids were equivalent to riffles, assuming forewaters and embayments were equivalent to backwaters, excluding any mesohabitats identified in side channels from the counts, and counting any connected pools, runs, and riffles as a single mesohabitat even when Moring et al. 2014 separated them. To account for varying flow level in the Heard et al. 2012 data, we averaged data from the lowest three months of flow as the low flow data points, averaged data from the middle 6 months of flow as the intermediate flow data points, and averaged data from the highest three months of flow as the high flow data points. Average flow from these months was mostly within the ranges of flow for high, intermediate, and low reported by Moring et al. 2014. We used the width data from the Castolon reach of Dean and Schmidt 2013 for the Santa Elena site, width data from the Johnson Ranch reach for the Johnson Ranch and gage at Johnson Ranch sites, and width data from the Boquillas reach for Hot Springs, Rio Grande Village, and above Boquillas canyon sites. We plotted all data from all sites and flow levels on one graph, and also plotted changes at the Santa Elena and Boquillas sites for each flow level. Boquillas data were the Rio Grande Village site from Moring et al. 2014, and the average of the Hot springs and above Boquillas canyon sites from Heard et al. 2012. Both the combined data and individual site changes generally support the model that habitat diversity increases with increases in channel width (Figures 5 and 6). However, this relationship should be explored further in the future, given the issues with data comparability between the two studies used, and also to refine the shape of the relationship between channel width and habitat diversity.

**Figure 5.** Relationship between channel width and number of mesohabitats. Data were compiled from Heard et al. 2012, Moring et al. 2014, and Dean and Schmidt 2013.
Physical Habitat-Aquatic Community Linkages

All else being equal, maintenance of the full native species community will most likely be achieved when physical habitat diversity is maximized, because all required habitats of all species will be available. However, the amount of different habitat types needed to support viable populations of different species is largely unknown in the Big Bend region and for aquatic species generally. In part, this is due to the influence of other factors besides habitat availability (discussed below). This makes it uncertain whether habitat diversity and availability necessarily needs to be maximized to ensure persistence of all native species.

An alternative focus to maximizing habitat diversity is to identify the most limiting habitat types for the rarest species or species of greatest conservation concern and identify the minimum amount of limiting habitat needed to sustain populations of these target species. Based on research in the Big Bend region and elsewhere, there are a number of different habitat types that may be particularly important for maintenance of the native community.

Fish habitat requirements

As mentioned above, shallow slow-velocity habitats are likely to be lost during periods of channel narrowing, and these types of habitats are critical for many species in the Big Bend region, particularly for early life stages of native fish (Heard et al. 2012, Garrett and Edwards 2014). For example, the Rio Grande silvery minnow is known to spawn in seasonally flooded habitats in the middle...
Rio Grande (Magaña 2012, Magaña 2013, Gonzales et al. 2014). Floodplain habitats appear to be important for this species for several reasons. First, they retain eggs (Medley et al. 2007, Gonzales et al. 2014), which otherwise could drift 100s of kms downstream in the main river current, often into unsuitable habitat such as reservoirs or the mouths of predators (Platania 1995, Platania and Altenbach 1998, Platania 2000, Dudley and Platania 2007, Zymonas and Propst 2009, Osborne et al. 2005, Widmer et al. 2012, Medley and Shirey 2013). Second, they provide warmer temperatures than the river channel during spring spawning, with temperatures optimal for growth and development, although this benefit may be negated if floods are provided by hypolimnetic dam releases (Platania 2000, Magaña 2012). Floodplain pools also tend to be highly productive due to light availability supporting autochthonous resources and high inputs of allochthonous resources (Magaña 2009, Magaña 2013). The high productivity further ensures rapid growth and development of vulnerable early life stages (Schlosser 1991), and may also provide ideal feeding locations for adults, which are known to consume organic matter and diatoms (Cowley et al. 2006, Shirey et al. 2008, Watson et al. 2009). They also tend to be free of larger-bodied predatory fish. Other slow-velocity habitats such as backwaters and embayments are also important, as they can provide similar habitats as floodplain pools in terms of egg retention, optimal temperatures, production, and reduced predator abundance (Dudley and Platania 1997, Platania 2000, Pease et al. 2006, Magaña 2009, Medley et al. 2007, Shirey et al. 2008, Moring et al. 2014). In the Big Bend region, where sediment accretion has raised floodplain surfaces above the channel bed, features within the channel, such as seasonally flooded channel bars and inset floodplain surfaces may provide floodplain-like habitat.

In the Big Bend region, studies of habitat preference have shown that Rio Grande silvery minnow use backwaters and embayments, shallow pools, silt to cobble-dominated runs, slow flow areas along cut-bank margins and shallow channel edges, and avoid swift-water riffles and deep pools (Edwards and Garrett 2013, Moring et al. 2014). Thus, the conversion of wide, shallow, sandy, braided channel form to a narrow, single-thread canal-like form has likely reduced available habitat for the Rio Grande silvery minnow (Bestgen and Platania 1991, Dudley and Platania 1997, Medley et al. 2007). Other native fish with similar life history characteristics as the Rio Grande silvery minnow, including the Tamaulipas shiner and the Rio Grande shiner, often co-occur with the Rio Grande silvery minnow and also likely use these types of habitats preferentially (Edwards and Garrett 2013, Garrett and Edwards 2014). Larger-bodied native fish such as the blue sucker are found most often in riffles and deep pools with substantial current (Garrett and Edwards 2014). Some smaller bodied species, including the speckled chub and longnose dace have also been associated with riffle to run habitats with gravel substrate (Heard et al. 2012).

Many fish species have been found to congregate in areas where spring systems flow into the Rio Grande channel (Garrett and Edwards 2014). These springs and groundwater upwelling areas may serve as critical refuges from drought conditions and elevated temperatures, and in some cases harbor species that do not occur in the mainstem river, including several macroinvertebrates (Baumgardner and Bowles 2005). For example, although Rio Grande silvery minnow typically prefer shallower slow-flowing habitats, they may use deep pools with upwelling hyporheic water and overhead cover during dry periods and during cold temperature periods in winter (Dudley and Platania 1997, Cowley et al. 2006). Temporary flow in ephemeral tributaries also provide important breeding and rearing habitat for many native fish species (Hubbs and Wauer 1973), and these tributary flows also support a unique fauna compared to the mainstem river (Hubbs et al. 1977, Miyazono and Taylor 2013a). Research on other
desert river systems has found that even large-bodied fish use tributaries seasonally, likely for spawning and foraging activities, and management of tributaries will thus play an important role in native fish conservation (Bottcher et al. 2013).

**Mussel habitat requirements**

Freshwater mussels, another group of conservation concern in the region, are likely to have different habitat requirements than Rio Grande silvery minnow and other pelagic spawning minnows. Though less is known about mussel habitat requirements in the region, recent surveys have suggested that cracks and overhangs in submerged bedrock are key habitats for freshwater mussels (Jeff Bennett, personal communication). Mussel species known to occur on the Rio Grande downstream of the Lower Canyons reach, such as the Texas hornshell, have been found in microhabitats such as where bedrock and boulders interface with clay substrate in riffles and along undercut banks (Karatayev et al. 2012, Inoue et al. 2014). Similar habitats as native fish may include shallow silty and sandy bars near gravel riffles (Karatayev et al. 2012, Mabe and Kennedy 2014).

**Non-native species issues**

An important consideration in identifying critical habitats for native species is the potential use of these same habitats by non-native species, that may negatively interact with native species. Although many species of non-native fish have more general habitat requirements than sensitive native species, there is likely to be overlap in habitat use between native and non-native species. For example, competition with non-native plains killifish may have reduced population densities and limited distributions of native fish using isolated flows in tributary systems (Hubbs and Wauer 1973, Miyazono and Taylor 2013b). Early life stages of non-native fish are likely to use similar slow-velocity habitats as native fish, to obtain the same benefits as native fish.

**Hydrologic-Aquatic Community Linkages**

Hydrologic forcing events, including floods and droughts impact the aquatic community by altering the physical habitat of the river. Hydrologic events also influence aquatic communities directly.

**Negative effects of floods**

Large flood events, such as reset floods, can mobilize gravel and cobble-size bed sediments, which constitutes a severe disturbance to benthic organisms such as macroinvertebrates, mussels, and algae (Davis 1980, Grimm and Fisher 1989, Allen and Vaughan 2010). The high flow velocities encountered in large floods can also sweep fish, especially young age classes, downstream when fish are not able to move to low-velocity refuges (Heard et al. 2012). Following flood recession, organic matter and fine sediments settle onto the streambed and can often stimulate high bacterial production, leading to low-oxygen conditions that may be detrimental to fish and other organisms. High algal biomass in river sections immediately below the Rio Conchos confluence are one source of abundant organic matter that can be transported and deposited downstream during floods (Porter and Longley 2011).

Smaller tributary-derived floods can also be detrimental to aquatic organisms, primarily due to the high sediment load carried by these floods. The delivery and settling of fine sediments in the Rio Grande channel can fill backwaters and other slow velocity habitats and reduce the availability of rearing habitat for young fish. An increase in silt-bottomed sediments is thought to be a major driver of changes
in fish communities throughout the Rio Grande in Texas (Edwards and Contreras-Balderas 1991, Contreras-Balderas et al. 2002). In addition, benthic organisms, such as mussels, may be covered over by fine sediments if flow velocities in the main channel are not sufficient to keep gravel and cobble beds clear (Winemiller et al. 2010, Inoue et al. 2014). The amount of fine sediment in gravel bars and riffles likely impacts the community composition of macroinvertebrates by decreasing complexity of interstitial spaces in coarse substrate (Davis 1980, P. Diaz, personal communication); for example, mayfly diversity may be limited by persistent muddy, low-flow conditions (Baumgardner and Bowles 2005). The sediment-laden water produced by tributary floods can also reduce algal biomass on the streambed through reduction in light availability (Porter et al. 2009, Porter and Longley 2011) – this can also lead to relatively low oxygen levels in the river by reducing primary production and may limit availability of zooplankton and macroinvertebrate prey resources, which are known to use algal resources and often fluctuate seasonally with algal availability (Bane and Lind 1978, Pease et al. 2006).

**Positive effects of floods**

Flooding and moderate dam release flows can also have direct positive effects on native aquatic communities. In other desert river systems, decline of native species has been tied directly to modification of flow regimes and particularly the reduced occurrence of large, long duration flood events (Budy et al. 2015). In the middle Rio Grande, the predictable spring flood events provide a spawning cue for many native species, including the Rio Grande silvery minnow (Platania and Dudley 2001, Turner et al. 2010). The relative importance of spring floods for spawning cues in the Big Bend region is less certain, and fish likely use other seasonal flow events as spawning cues as well (Platania and Dudley 2001, Edwards 2005). For example, the Rio Grande silvery minnow can potentially spawn successfully in highly turbid flows, such as flows generated by ephemeral tributary floods, because highly turbid conditions appear to trigger egg ripening in females and will keep eggs suspended above the river bed and prevent them from being buried by fine sediments (Platania 1991, Medley and Shirey 2013). Flooding also helps to maintain benthic habitat quality by flushing fine sediments from gravel bars and other coarse sediment deposits (Kondolf and Wilcock 1996). Removing fine sediments helps to prevent clogging of interstitial spaces in gravel, that are used by macroinvertebrates and by some fish as egg nurseries. Reduction in fine sediments on the bed also promotes hyporheic exchange flows, flows that move through subsurface sediment, and these flows provide ecological benefits such as cool upwelling water and nutrient exchange (Hester and Gooseff 2010). Floods in ephemeral tributaries support isolated pool and channel habitat in mostly dry streams, which provide temporary breeding and rearing habitat for many native fish species (Hubbs and Wauer 1973).

**Effects of dam release flows**

Dam releases likely benefit aquatic communities by improving water quality, stimulating primary production and thus oxygen production through increased light availability (Porter et al. 2009, Porter and Longley 2011), maintaining a greater amount and diversity of habitat, and reducing drought impacts. However, the timing of releases may be critical. If releases occur after a period of low flows, accumulated fine sediment and organic matter on the river bed may be suspended into the water column and stimulate bacterial production and consumption of oxygen.

**Effects of spring and groundwater inputs**

Springs and groundwater inputs have a similar impact as moderate dam release flows (Lambert et al. 2008, Bennett 2011, Porter and Longley 2011, Raines et al. 2012), and are especially important
during hot, dry periods by providing refuges from high temperatures and often poor water quality that can persist when flow levels drop.

**Drought effects**

River drying is another major hydrologic disturbance event that impacts aquatic communities in the Big Bend region. In the 1950s, both the Rio Conchos and upper Rio Grande basins experienced drought conditions (Woodhouse et al. 2012). The relatively unusual occurrence of coincident drought caused the river to go completely dry on occasion, and this river drying is thought to be a major factor in the extirpation of the Rio Grande silvery minnow from the Big Bend reach (Edwards 2005). In addition, the drought likely contributed to extirpation of native species from the Rio Grande in New Mexico and further downstream in Texas (Bestgen and Platania 1990, Contreras-Balderas et al. 2002). Sampling of the fish community before and after a drought in 2003 showed significant alterations to the fish community in many reaches, including a shifting of dominance by small bodied minnow species to larger species including catfish and gar (Moring 2005). The shift was attributed to low oxygen conditions (Moring 2005), but there is some indication that the Rio Grande silvery minnow forages in relatively low-oxygen environments (Cowley et al. 2006), and other causes for the shift could not be excluded. Reductions in large-bodied benthic fish such as the blue sucker may be tied directly to loss of deep, swiftwater habitat with reduced flow (Edwards and Contreras-Balderas 1991, Garrett and Edwards 2014), and many mussel species are intolerant of lentic-like conditions that may be prevalent during low flow (Burlakova et al. 2011b). Flow level declines necessarily limit the available area for benthic organisms and primary production, although the habitat diversity may be higher in moderately low flow conditions compared to high flow conditions (Moring et al. 2014). Drying of the river to isolated pools can reduce connectivity between habitats and impede movement of aquatic organisms, potentially isolating populations and increasing their vulnerability to extinction (Inoue et al. 2015). Low flows also often lead to sediment accumulation on the riverbed, as velocities are insufficient to keep fine sediment mobilized. The accumulation of fine sediment and organic matter on the riverbed can reduce oxygen in the water column through increased decomposition of organic matter. Anoxic sediments with available organic matter are favorable sites for methyl mercury production, a mercury compound that is particularly bioavailable, and the occurrence of these conditions may be partly responsible for relatively high and potentially harmful concentrations of mercury in fish in the Big Bend region (Smith et al. 2010). Temperatures may also exceed thermal tolerances for many organisms during hot and dry periods.

**Drought effects on water quality**

Water quality also tends to decline with lower flows (Passell et al. 2007). Longitudinal studies of the Rio Grande in the Big Bend region have shown a general pattern of decreasing salinity and nutrient concentrations from upstream to downstream as springs and groundwater inputs raise discharge levels through the reach (Bennett 2011, Porter and Longley 2011, Raines et al. 2012, Miyazono et al. 2015). The shifting water quality conditions were shown to control the community of algae found in the river (Porter and Longley 2011). Brackish planktonic diatom species and dense *Cladophora* mats dominated upstream areas where salinity and nutrients were high and groundwater was characterized as a sodium-sulfate type. Benthic diatoms and even red algae became more prevalent downstream as calcium bicarbonate increased and salinity and nutrients decreased. Increasing salinity has been implicated in shifting abundances of native fish species throughout the Rio Grande in Texas (Edwards and Contreras-Balderas 1991, Contreras-Balderas et al. 2002, Miyazono et al. 2015). The fish fauna in the region has been divided into distinct low-diversity saline and diverse non-saline assemblages, as well a tributary-
dependent assemblage (Hubbs et al. 1977). Decreasing flows and increasing salinity have been linked to a shift from saline intolerant species such as speckled chub, Rio Grande shiner, and longnose dace to saline-tolerant species such as red shiner (Miyazono et al. 2015). Salinity affects the size and density of Rio Grande silvery minnow eggs and thus, exceptionally high salinities during dry periods could potentially reduce reproductive success of this and other species (Cowley et al. 2009), though salinities sufficient to reduce reproductive success have not been observed in the Big Bend reach.

Biotic Interactions

In addition to the physical constraints of habitat availability, flow disturbances, and water quality, biotic interactions are likely to play a major role in structuring the distribution and composition of aquatic communities. Disease and parasitism has been little explored in shaping biotic communities in the region, though some research suggested tapeworm parasitism could pose a barrier to successful Rio Grande silvery minnow reintroduction (Bean et al. 2007, Bean and Bonner 2010), and Texas hornshell populations in the Black River, New Mexico were parasitised by a dragnofly larva (Levine et al. 2009).

Non-native species impacts

Predation and competition from non-native species are likely to limit the abundance and distribution of native fish and invertebrates (Anderson et al. 1995). Although the Big Bend region is relatively low in non-native fish abundance compared to other rivers in the region (Heard et al. 2012), the presence of non-native species, such as common carp and plains killifish, and nearby source populations of other non-native fish constitutes a potential future threat to native fish diversity. For example, the colonization and rapid population expansion of plains minnow was thought to be a major factor in the extirpation of the Rio Grande silvery minnow in the Pecos River, through both competition and hybridization (Cook et al. 1992, Bestgen and Probst 1996, Moyer et al. 2005, Hoagstrom et al. 2010b). Non-native species often occupy similar habitats as native species or may be habitat generalists (Hoagstrom et al. 2010b), and thus, any habitat improvements made on the river may potentially benefit non-natives equally or to the expense of native species (Walsworth and Budy 2015). Similarly, non-native species may be able to take advantage of managed flows or disturbance events such as droughts to increase their abundance at the expense of native fish. Continuing with the Pecos River example, modified flows, in particular reduction in spring snowmelt floods and increased occurrence of low flows, likely facilitated the colonization and rapid expansion of the plains minnow, which was more tolerant of drought conditions (Hoagstrom et al. 2010b). Non-native species often occupy similar niche space as native species, and can compete strongly for similar resources with native species, particularly where physical habitat has been simplified (Walsworth et al. 2013).

In addition to non-native species, shifts in the abundance of native species may limit recovery of rare native species such as the Rio Grande silvery minnow. Increasing salinity and altered habitat in the Rio Grande has been linked to shifts in abundance of native species, in particular, there has been an increase in tolerant red shiner, whereas several other shiner species have declined (Garrett and Edwards 2014, Miyazono et al. 2015). The strong competition from high abundances of red shiner may potentially pose a barrier to recovery of rare shiner species, especially since these species have similar habitat requirements and life history strategies to many rare native species. For example, Rio Grande silvery minnow were not frequently caught in habitats where red shiners were present (Edwards and Garrett
2013), and the native fish fauna in the middle Rio Grande was found to have broadly overlapping diets and habitat preferences (Dudley and Platania 1997, Turner et al. 2010).

Shifting abundance of native species

Extirpation or shifts in abundance of native fish species could potentially be a major limiting factor for native mussel species, because mussels require fish hosts for dispersal and to complete their life cycle, often using one or a few species as hosts (Barnhart et al. 2008, Winemiller et al. 2010, Burlakova et al. 2011a, Karatayev et al. 2012). Large-bodied benthic-foraging fish may be particularly important to mussel species, because they often disperse long-distances and are likely to come in contact with mussel beds (Levine et al. 2012). For example, the native river carpsucker (*Carpiodes carpio*) was found to be a very important host species for native mussels in the Black River, New Mexico, even though it was not the most abundant species (Levine et al. 2012). Non-native species can potentially provide a suitable host for mussels, but this is not always the case, especially if mussels have specific host requirements or if behavior of the non-native species brings it in contact with mussel beds less often than an equivalent native species (Barnhart et al. 2008, Levine et al. 2012).

Food web interactions

Macroinvertebrates and algae provide the food base for native fish species, and reduction in primary or secondary production, whether through poor water quality, limited habitat availability, or direct disturbance events, is likely to limit the abundance and population sizes of native fish, which can increase the potential for extirpation of rare species. In addition, shifts in the community composition of algal or invertebrate communities can be detrimental to native fish, if fish are heavily reliant on a particular component of these communities for their diet. For example, diet analysis of Rio Grande silvery minnow in the middle Rio Grande has shown a preference for benthic diatoms during non-flood periods (Cowley et al. 2006, Shirey et al. 2008, Magaña 2009, Watson et al. 2009, Magaña 2013), a community that was not very common in upper reaches of the Big Bend region (Porter and Longley 2011).

Critical Data Gaps

As the above literature review shows, there has been substantial research effort undertaken to understand the Rio Grande ecosystem in the Big Bend region, and the physical, chemical, and biological processes that structure aquatic communities. This understanding provides an important foundation to build from over the next several decades in terms of furthering understanding of the river ecosystem and its controlling processes. With continued interest in conservation and restoration of the river ecosystem in Big Bend, there is an opportunity to develop a strategic, coordinated scientific monitoring and research plan that can address important knowledge gaps in current understanding and thus provide information that will be most useful to management of the aquatic resources in the coming years.

We have highlighted some of the major unknown or uncertain relationships between physical and biological attributes of the river ecosystem in the conceptual diagrams of the two major reaches in the Big Bend region (Figures 2 and 3). These are not the only important data gaps in understanding of the river ecosystem, but highlight particularly important gaps for river managers. Many of the uncertain
relationships are in the linkages between the physical and biological components (Schmidt and Dean 2011, URGBBEST 2012). For example, it is fairly well understood how hydrologic forcing events shape the geomorphic properties of the Rio Grande channel, but the impacts on overall habitat diversity and specific habitat types are less well known. Similarly, the habitat requirements of many individual fish and invertebrate species have been well studied, but how populations respond to shifting arrangement and abundance of these habitats as driven by channel morphology changes is less well known. This is particularly true for the Lower Canyons reach.

**Expert Opinion Survey**

Based on development of the conceptual models, the literature review, and discussions with local experts, we formulated a list of 10 research questions regarding aquatic resources in the region that are currently uncertain or unaddressed (Figure 7). Although it would be ideal to address all these questions, the limitations of time and money necessitate a narrowed focus on the most critical unknowns over the next several years to decades. To help identify these critical gaps, we solicited expert opinion from those most knowledgeable with the system. Using an online survey form, we asked experts to rank the 10 questions in terms of how important it was to address the questions over the next 5-10 years.

Respondents represented the Fish and Wildlife Service (33% of respondents), U.S. Geological Survey (33%), Texas Parks and Wildlife (11%), National Park Service (11%), and Universities (11%). Most respondents had either geomorphology (33% of respondents) or fish ecology expertise (45%), but invertebrates and general aquatic ecology (11%) and hydrology and water quality (11%) were also represented. Respondents had an average of 14 years’ experience working on the river system.

Most respondents agreed that identifying primary limiting factors for native aquatic biota in the region was an important knowledge gap to address over the next 5-10 years (Figure 7). The potential for non-native fish to respond more strongly to habitat changes than native fish and potential differences in geomorphic response to hydrologic forcing events between the alluvial floodplain reaches and the Lower Canyons reach were consistently ranked as lower importance compared to other knowledge gaps (Figure 7), though one respondent did rank the former question as highest priority. Additional questions not posed in the survey, but raised by the respondents included the need to identify environmental flow specifications and sediment impacts on food resources, as well as the need to focus on maximizing available habitat rather than identifying the minimum habitat needed to support populations.

The expert opinion survey provides important guidance for developing future aquatic resource monitoring protocols. Foremost, the general consensus that primary limiting factors for native fish and other aquatic organisms still require research suggests there is a need to consider multiple potential controls on aquatic communities, including habitat limitations, hydrologic forcing events, water quality impacts, and biotic interactions. Thus, overall, it would be useful to develop specific research and monitoring projects under a general model that considers multiple working hypotheses and can integrate data from disparate sources, such as flow measurements, water quality measurements, channel width, habitat, and fish assemblages, in a common analysis framework. In the section below, we propose one such hypothetical framework, provide an example of how it can be applied to the Rio Grande in Big Bend, and suggest research approaches that would best be integrated under this general
framework. If specific questions are addressed within this general framework, the information gained would not only help address the specific question under investigation, but also contribute to general knowledge regarding the important limiting factors for aquatic biota in the river. Specific research questions that experts generally agreed were of high priority included the general direct impacts of hydrologic forcing events on aquatic biota (Question 4), including the importance of flash floods for spawning of Rio Grande silvery minnow and other native fish (Question 2), the relationship between habitat complexity and food availability (Question 5), and the relative importance of water quality versus water quantity (Question 9).

1. Does habitat complexity change predictably with geomorphic organization?
2. Can silvery minnow and other pelagic spawning fish recruit successfully during short-lived tributary-derived high flows?
3. What is the minimum amount of habitat needed to sustain populations of silvery minnow and other native fish?
4. How do different hydrologic events directly impact biotic communities?
5. Is there a predictable relationship between habitat complexity and availability of food resources for native fish?
6. Do non-native fish respond more strongly to habitat changes than native fish?
7. Does geomorphic organization of the Lower Canyons reach respond to hydrologic forcing events in the same way as the alluvial floodplain reaches?
8. Do biotic communities respond similarly to hydrologic forcing events in the Lower Canyons and alluvial floodplain reaches?
9. Is water quality or water quantity more important for biological communities?
10. What is the primary limiting factor for native fish and mussels in the region?

![Figure 7. Average ranking score for 10 research questions regarding aquatic resources on the Rio Grande in Big Bend. Experts were asked to rank the questions from 1 to 10, with 1 being the most important question, 10 the least. Score for each question is the average ranking among all responses, subtracted from 11, so that higher scores indicate a higher average ranking, i.e., the higher the score, the more respondents felt it was a top priority research question.](image)
Recommended Framework for Aquatic Monitoring Efforts

Although the relative influence of different limiting factors on native aquatic biota is not certain, this can be parsed out using an appropriate sampling framework and analysis methods. In particular, the need to address multiple different limiting factors requires a coordinated effort to collect multiple data types at the same locations and near the same time. A coordinated effort would involve several components:

- Development of standard protocols that can guide different groups sampling in different locations and at different times. This would help ensure the data collected is comparable across time and between sites. Lack of comparability partially limits integration of previously collected data and analyses that could be performed on this historical data. For example, different habitat sampling methods in the Heard et al. 2012 and Moring et al. 2014 studies made the integration of these two studies in examining width-habitat complexity relationships difficult (Box 1).

- A set of 3-5 sites in both the alluvial floodplain and Lower Canyons reaches where measures of discharge, water quality, channel geomorphic changes, habitat mapping, and riparian vegetation and biotic community surveys are conducted regularly. Much of this data is being collected currently by different groups, but if multiple sites are established where these efforts coincide, the different data collection efforts could be more easily integrated. Ideal locations for these coordinated monitoring sites would be at established flow and water quality monitoring gage locations, such as Castolon, Johnson Ranch, and Foster’s Ranch, at sites with relatively easy access, and at sites that have been repeatedly surveyed in the past, such as Santa Elena Canyon (Terlingua Creek mouth), Rio Grande Village, the Boquillas area, and Dryden Crossing. In the alluvial floodplain reach, locating sites between Santa Elena and Boquillas would be ideal, because sediment budgeting analyses are ongoing within this stretch (Dean et al. 2016).

- Collection of diverse data sources within a relatively narrow timeframe. Given the dynamic nature of the Rio Grande, collecting habitat, geomorphic, and biotic data simultaneously would reduce uncertainty in any attempts to develop relationships between biotic communities and physical components of the ecosystem.

- Regular and seasonally consistent sampling at each site. The purpose of repeated sampling at designated sites is to track changes in biotic communities over time and relate these changes to limiting factors, thus regular sampling captures more detail in changing conditions and seasonally consistent sampling reduces uncertainty associated with the season of collection. The best frequency of repeated sampling will vary by data source, but at least annual sampling for many parameters will be necessary to capture changes and relate them to limiting factors.

Importantly, this framework of coordinated efforts at several sites does not preclude additional work, such as longitudinal sampling of biotic communities and habitat properties, or targeted investigation of limiting factors for Rio Grande silvery minnow. Rather, it ensures that any sampling efforts can be integrated into a unified analysis of biotic communities and their limiting factors, and thus contribute towards greater understanding of the Big Bend ecosystem and hopefully, improved management. A potential additional benefit of coordinated sampling is the future reduction of data collection efforts for
some parameters if strong correlations between parameters are found. For example, if the relationship between channel width and habitat diversity holds up to additional analysis (Box 1, Figures 5 and 6), it may be possible to eliminate measures of habitat diversity and regularly collect the much less time-intensive predictive parameter channel width.

The general framework of a coordinated monitoring program at multiple established study sites has been recommended previously (Schmidt and Dean 2011, URGBBEST 2012). Thus, we take an additional step and provide an example of one possible analytical approach that could be used in the future to integrate data. We use available data from the Santa Elena, Castolon, Rio Grande Village, and Boquillas sites and use a structural equation modeling approach to explore the relative influence of different limiting factors on native fish richness and abundances of several native fish species.

**Structural Equation Modeling: An Example**

Structural equation modelling is a statistical technique that uses correlations among observed variables to infer the relative importance of predictor variables, which may be unobserved or latent variables, on a dependent variable, which may also be a latent variable. The technique has roots in path analysis, making it well suited to explore causal relationships, for use with variable ecological data in general, and thus can be used to capture relationships between physical and biological components of an ecosystem as conceptualized for the Rio Grande (Figures 2 and 3). The technique has been applied in river ecosystems previously to investigate the relative importance of different controls on nitrate uptake (Hall et al. 2009), and to explore the relative importance of non-native species and habitat degradation in driving extinction of freshwater fish in the Mediterranean (Hermoso et al. 2011), among other applications.

We developed a structural equation model to capture and investigate the relative influence of geomorphic properties/physical habitat, water quality, non-native fish, and direct hydrologic forcing on aspects of the native fish community. The model structure was a simplification of the overall conceptual model for the Rio Grande alluvial reach (Figure 2). Fish data were compiled from sampling campaigns that targeted the Terlingua Creek Mouth/Santa Elena/Castolon area and the Rio Grande Village/Boquillas area and included Heard et al. (2012), Garret and Edwards (2013), Moring et al. (2014), and data provided by Ken Saunders of the Texas Parks and Wildlife Department. Water quality was represented as a latent variable (a variable not directly measured but assessed with several indicator variables) with two indicator variables: conductivity and sulfate. These variables were chosen, because the reach is listed as impaired for chloride, sulfate, and total dissolved solids, salinity is known to influence fish communities, and salinity, nutrients, and sodium-sulfate chemistry are known to influence the algal community of the river (Hubbs et al. 1977, Porter and Longley 2011, Miyazono et al. 2015). Direct hydrologic forcing was represented as a composite variable, which is similar to a latent variable, except that the indicator variables are assumed to control the composite variable, rather than being manifestations of the latent variable (Grace and Bollen 2008). Hydrologic forcing in our model was controlled by four variables: flow on the day of fish sampling, the median and minimum flows over the previous 90 days, and the number of flow spikes over the previous 90 days (a flow spike was defined as a rise of at least 1.5 times the previous day’s flow based on mean daily discharge, but with multiple spikes during one event excluded). These variables were chosen to represent flow during sampling and
to capture effects of some major flow components: drying events (higher minimum flows in the last 90 days indicate that river drying did not occur), baseflows (greater median flows indicated more consistent maintenance of high flow levels, potentially through dam releases), and tributary-derived flash floods (number of flow spikes). Geomorphic properties and physical habitat were represented by active channel width, because this was the main geomorphic variable consistently available for the alluvial reach for each fish sample. Non-native fish abundance was included as the summed relative abundance of common carp, inland silverside, and plains killifish, the most common non-native fish in the region.

We analyzed separate models with native fish species richness and relative abundance of Tamaulipas shiner, river carpsucker, and red shiner as the response variable. We chose these three species as representatives of the pelagic, small-bodied fish community, the benthic large-bodied community, and the habitat generalist, water quality tolerant community. Data from the Terlingua Creek Mouth/Santa Elena/Castolon area and the Rio Grande Village/Boquillas area were combined to increase sample size, but these sections could be separated in the future as data become available.

Model results: Native fish species richness

The model results suggest that active channel width was the most influential variable, relatively speaking, in determining native fish species richness (Figure 8). The effect was in the expected direction, as native richness tended to increase with increases in channel width. This could potentially reflect an increasing diversity of habitats as channel width increases. Neither non-native abundance, water quality, nor hydrologic forcing had a strong influence on native fish species richness, relative to channel width.

Model results: Tamaulipas shiner relative abundance

Hydrologic forcing had the strongest effect on Tamaulipas shiner, but nonnative relative abundance, water quality, and channel width were also important variables (Figure 9). Relative abundance of Tamaulipas shiner showed negative relationships with all four variables, suggesting that relative abundance declines as nonnative species increase and water quality decreases (conductivity and sulfate increase). The negative relationship of Tamaulipas shiner with hydrologic forcing is complicated by the fact that flow on the day of sampling and number of flood spikes show an opposite direction of influence on hydrologic forcing as median and minimum flow over the previous 90 days. The directions of influence suggest that Tamaulipas shiner relative abundance tends to decline with increases in flow on the day of sampling and the number of flood spikes over the previous 90 days, whereas relative abundance tends to increase as median and minimum flows over the previous 90 days increase.

Model results: River carpsucker relative abundance

Water quality had the strongest influence on river carpsucker relative abundance, with hydrologic forcing having a lesser influence and nonnative relative abundance and channel width having very weak influence. The model results suggest that as conductivity and sulfate increase, carpsucker relative abundance increases. This is opposite of the expected direction, but is not necessarily indicating that carpsucker abundance increases with declining water quality. The response may be due to water quality reducing abundance of other species more than carpsucker and thus increasing the relative abundance of carpsucker. Carpsucker were responding to hydrologic forcing oppositely as Tamaulipas shiner, but as mentioned above, the relative influence of hydrologic forcing was less for river carpsucker.

Model results: Red shiner relative abundance

All independent variables had a relatively equal influence on relative abundance of red shiner. Red shiner relative abundance tended to decrease with nonnative species abundance, and increase with
channel width. As expected given their status as a water quality-tolerant species, increases in sulfate and conductivity tended to increase red shiner relative abundance. Red shiner relative abundance also responded oppositely to hydrologic variables as Tamaulipas shiner, that is relative abundance tended to increase with increases in flow on the day of sampling and number of flood spikes over the previous 90 days, and increase with declines in median and minimum flow over the previous 90 days.

Alternative models

One advantage of structural equation modeling is the ability to explore how particular causal relationships specified in the model impact the overall model fit and explanatory power. For example, in the models above, it is possible to eliminate the various indirect effects and ask how model fit and proportion of variance explained changes relative to the full model. If model fit and variance explained are not significantly altered, including indirect effects in the model may not be necessary to capture the main sources of variation. If model fit decreases, indirect effects are likely important.

Using the Tamaulipas shiner model, we systematically eliminated the indirect effects of hydrologic forcing on water quality and the indirect effects of hydrologic forcing and water quality on nonnative abundance and explored how model fit and proportion of explained variance in Tamaulipas shiner relative abundance changed (Table 2). Removing the effect of hydrologic forcing on water quality clearly gave a poorer model fit and lower proportion of explained variance, suggesting that the influence of hydrologic forcing on water quality is an important control on the relative abundance of Tamaulipas shiner. In contrast, removing the effects of hydrologic forcing on nonnatives improved model fit without substantially altering the proportion of explained variance, suggesting this is not an important relationship for explaining the relative abundance of Tamaulipas shiner. The effects of water quality on nonnative relative abundance is similarly unimportant in explaining Tamaulipas shiner relative abundance, given that neither model fit nor proportion explained variance declined substantially when the effect was removed. This result is further confirmed by the fact that eliminating both the effect of water quality and hydrologic forcing on nonnative relative abundance substantially improved model fit without sacrificing substantial explanatory power. These results suggest that nonnative relative abundance is varying independently of water quality and hydrologic forcing, as least as it relates to the impact on Tamaulipas shiner.

The ability to test the removal of different relationships specified within structural equation modeling also highlights the fact that an infinite number of potential models could be specified to capture the relationships between independent variables and the response variable of interest. Thus, the models presented in Figures 8-11 are only one specification of the ways that water quality, hydrologic, habitat, and nonnative species variables could be impacting native fish species. Other model specifications and inclusion of other independent variables could and should be discussed as more data become available in the future. For example, it could be argued that each of the hydrologic variables has unique effects on fish assemblages and should be modeled as independent variables and not lumped into one composite hydrologic forcing variable. The ability to specify and test these different specifications is one advantage of structural equation modeling and facilitates a frank discussion of the known and assumed but untested relationships operating in the region.

Model caveats

The models should be viewed as a preliminary exploration of the relative effects of flow, habitat, water quality, and nonnative fish – an example of what can be done, and not a definitive conclusion on
relative effects. As explained above, the models presented are only one specification of how flow, habitat, water quality, and nonnative fish may be impacting native fish; other specifications may be equally valid, and there may be other variables that need to be considered. In addition, the model results should be considered preliminary given the limited sample size (53 fish samples), limited metrics of habitat, and the combined data sets from two different sites on the river. The latter in particular may be responsible for the counterintuitive relationship between water quality and river carpsucker relative abundance mentioned above. River carpsucker relative abundance is on average higher in the Santa Elena/Castolon reach, where conductivity and sulfate are also higher, compared to the Rio Grande Village/Boquillas reach. Additional sampling will allow separate analyses for each site and may modify the relationships presented here.

Another important caveat of the models is that they are derived from data collected at sites in the alluvial reach of the Big Bend region, and thus modeled relationships are likely to differ in the canyon reaches within the region. For example, it is possible that habitat variables such as active channel width would have a lesser influence in canyon sections, given that channel width and associated habitat complexity changes have likely been of lower magnitude in the canyon sections. Additional sampling of canyon reaches would allow comparison to alluvial reaches and would help determine whether biotic communities in the canyon sections are responding uniquely to physical changes.

We provide these models as an example of the kinds of analyses that can be done if measurement of flow, channel physical properties, water quality data, and biotic community sampling are coordinated under one guiding framework. If an aquatic monitoring program is structured in this way, these types of models can give insight into the relative effects of different driving variables, one of the major questions in the Big Bend region.

**Table 2. Model fit statistics and proportion of explained variation in Tamaulipas shiner relative abundance for different formulations of the Tamaulipas shiner model.** The first row gives fit statistics under the full model presented in Figure 9. Subsequent rows show fit statistics with different indirect effects removed from the model. Fit statistics are the chi-squared test ($\chi^2$), comparative fit index (CFI), Tucker-Lewis index (TLI), root mean square error of approximation (RMSEA), Akaike’s information criteria (AIC), and proportion of explained variance of Tamaulipas shiner relative abundance ($R^2$).

<table>
<thead>
<tr>
<th>Model</th>
<th>$\chi^2$ (Higher is better)</th>
<th>CFI (Higher is better)</th>
<th>TLI (Higher is better)</th>
<th>RMSEA (Lower is better)</th>
<th>AIC (Lower is better)</th>
<th>$R^2$ (Higher is better)</th>
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</thead>
<tbody>
<tr>
<td>Original</td>
<td>0.06</td>
<td>0.887</td>
<td>0.790</td>
<td>0.112</td>
<td>3326</td>
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<td>0.337</td>
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<td>3345</td>
<td>0.25</td>
</tr>
<tr>
<td>Hydrologic forcing to nonnatives (-)</td>
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<td>0.894</td>
<td>0.816</td>
<td>0.105</td>
<td>3324</td>
<td>0.33</td>
</tr>
<tr>
<td>Water quality to nonnatives (-)</td>
<td>0.04</td>
<td>0.864</td>
<td>0.765</td>
<td>0.119</td>
<td>3325</td>
<td>0.33</td>
</tr>
<tr>
<td>Both hydrologic forcing and water quality to nonnatives (-)</td>
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<td>0.948</td>
<td>0.900</td>
<td>0.088</td>
<td>3307</td>
<td>0.31</td>
</tr>
</tbody>
</table>
Figure 8. Structural equation model with native fish species richness as the response variable. Boxes are variables included in the model. Water quality is modeled as a latent variable, a variable not directly observed, but manifested by indicator variables sulfate (SO₄) and conductivity. Hydrologic forcing is modeled as a composite variable, a latent variable controlled by the variables flow on day of sampling and median flow, minimum flow, and number of flow spikes over the previous 90 days. Boxes with numbers along arrows indicate the standardized coefficients between variables. The lowest box connected to native richness gives the error variance, which subtracted from 1 gives proportion explained variance (R²). The bottom row of numbers gives the direct effects of active channel width, water quality, nonnative relative abundance, and hydrologic forcing on native fish species richness. The next higher set of numbers shows the effects of hydrologic forcing on water quality and nonnative abundance, and the effect of water quality on nonnative abundance. The top row of numbers indicates the relative contribution of indicator variables to the latent variables, with higher numbers indicating a higher correlation with (water quality) or relative influence on (hydrologic forcing) the latent variable. Note that numbers at different levels are not directly comparable, because they are relative indicators of different components of the model. Number of observations = 53. Chi-squared p-value = 0.01. CFI = 0.820. TLI = 0.666. RMSEA = 0.139.
Figure 9. Structural equation model with Tamaulipas shiner relative abundance as the response variable. See Figure 8 caption for a description of model interpretation. Number of observations = 53. Chi-squared p-value = 0.06. CFI = 0.887. TLI = 0.790. RMSEA = 0.112.
Figure 10. Structural equation model with river carpsucker relative abundance as the response variable. See Figure 8 caption for a description of model interpretation. Number of observations = 53. Chi-squared p-value = 0.09. CFI = 0.894. TLI = 0.802. RMSEA = 0.101.
Figure 11. Structural equation model with red shiner relative abundance as the response variable. See Figure 8 caption for a description of model interpretation. Number of observations = 53. Chi-squared p-value = 0.02. CFI = 0.858. TLI = 0.736. RMSEA = 0.128.
Recommendations for Investigating Factors Limiting Rio Grande Silvery Minnow Recovery and Native Fish Community Persistence

Rio Grande silvery minnow (*Hybognathus amarus*) was once one of the most abundant fish throughout the Rio Grande, but became restricted to a section of the middle Rio Grande in New Mexico representing less than 10% of its historic range (Bestgen and Propst 1996, Hubbs et al. 2008). Recently, efforts have begun to reintroduce the Rio Grande silvery minnow into the Big Bend region (Edwards and Garrett 2013), but the minnow is still rare in fish collections throughout the region. Thus, a critical question of management concern is why there are apparently so few Rio Grande silvery minnow in the Rio Grande today?

There are two potential reasons for the rarity of the silvery minnow. One is that it is actually fairly abundant but has not been detected in large numbers, and the other is that survival or recruitment or both are limited. Below, we outline a series of investigations that would help systematically narrow the potential limiting factors for Rio Grande silvery minnow in the region while simultaneously elucidating potential limiting factors for the native fish community as a whole (summarized in Figure 12). Some of this work can be conducted as part of the general monitoring framework proposed above, but other work will require some more specific, unique analyses. Efforts to conduct many of the analyses outlined below are already being conducted by Texas Parks and Wildlife and others or are planned for future trips (K. Saunders, personal communication). Thus, in part the outline provides a summary and rationale for these ongoing investigations. Other efforts will require time and money beyond the resources of the agencies currently working in the region.

**Hypothesis 1: There are Rio Grande silvery minnow present, but sampling effort has been insufficient to detect them at presumably low densities across a large spatial extent**

To rule out this possibility, an extensive fish sampling campaign should be conducted across a large spatial extent. This could be done as a focused trip on several river sections that would use several sampling techniques, and intensively sample known and likely areas of high habitat suitability. Techniques to use include:

- Canoe electroshocker
- Trap nets
- Minnow traps
- Seining
- Light traps (dependent on turbidity)
- eDNA – this is a technique to detect DNA from a target species in a water sample – it would require development and testing of a sampling protocol to be effective, but is very sensitive to low densities of individuals when used properly and requires minimal sampling effort, because only a water sample needs to be collected.

Measurements of habitat availability and use by any silvery minnow captured during an intensive sampling campaign would additionally yield valuable information on silvery minnow habitat preferences in the Big Bend region. Conducting this research at coordinated study sites, among others, as suggested above, would also add to the general understanding of physical-biotic relationships in the region.
Furthermore, identifying where silvery minnow are most abundant in the river would help in addressing the hypotheses below, because investigations would ideally be conducted where silvery minnow are known to be present, compared to where they are known to be absent. Current sampling efforts have targeted the minnow and have not found them in high abundance consistently at any site, suggesting they are indeed rare in the river. If no sites are found with consistent catches of Rio Grande silvery minnow, sites to address hypotheses below may need to be chosen based on known habitat preferences of Rio Grande silvery minnow.

Hypothesis 2: Stocked fish are not surviving or reproducing in the Big Bend region

There are a number of factors that could limit survival and reproduction of silvery minnow.

Hypothesis 2a: The stocked fish are not properly adapted to the Big Bend environment, or the current environmental conditions in the region are unfavorable for Rio Grande silvery minnow survival and reproduction

A stocking program to supplement the Rio Grande silvery minnow population in New Mexico has been ongoing for over a decade, and fish stocked in that region have survived and reproduced successfully, maintaining overall genetic diversity despite a small effective population size (Osborne et al. 2012). In addition, facilities that raise fish for stocking are tested for disease prior to fish release, and no fitness issues have been found with fish released into controlled hatchery environments, including outdoor ponds in Texas (M. Montagne, USFWS, personal communication). Thus, the condition of fish should be suitable for survival in the Big Bend region; however, it is possible that stocked fish are naïve or poorly adapted to local conditions, given that all stocked fish originate from the New Mexico population. To investigate this possibility, it may be worth conducting genetic analysis of museum specimens of Rio Grande silvery minnow collected in the Big Bend reach and comparing the genetic profile of these fish to currently stocked fish, to determine if there are any genetic differences. In addition, holding some fish within pens or in screened areas within stocking locations for several weeks or months could help answer whether fish show signs of stress or immediate mortality when introduced to the novel environment of the Big Bend region.

Another approach would be to tag fish (e.g., with PIT tags), and set up passive integrated antennae (PIA) above and below points of stocking to see if fish disperse from the point of stocking. Although this option would require substantial time and resource investment, it could also help answer other questions regarding native fish movement and habitat use if fish captured during sampling programs are routinely PIT-tagged.

Alternatively, the environmental conditions in the region, such as salinity levels or temperature may limit survival and reproduction of stocked fish. Recent surveys for stocked fish have found highest abundances of the minnow in and near spring inputs (M. Montagne, USFWS, personal communication), which have higher water quality and often cooler temperatures than the main river, suggesting these spring inflow conditions are preferred over the main river. If minnows continue to be found around spring inputs, efforts will be made to measure the habitat, temperature, salinity, and other water quality parameters near spring inputs,
information that should help determine potential limiting conditions in the Rio Grande mainstem.

**Hypothesis 2b: Physical habitat is limiting.**

The issues with habitat degradation are well known in the Big Bend region, but as discussed above, habitat in some areas is improving as a result of non-native vegetation removal, and there are other potential limiting factors besides habitat availability. Thus, it will be important to further refine understanding of habitat suitability in different reaches of the river. Measuring habitat properties of sampled reaches and properties of habitat where Rio Grande silvery minnow are captured will help develop habitat suitability indices for the minnow. This can be done as part of the intensive sampling efforts recommended above, and can be accomplished as part of the general recommended monitoring plan, especially if some sites are chosen that are likely areas for Rio Grande silvery minnow occupancy. A protocol for conducting habitat work has been developed and implemented by the Texas Parks and Wildlife Department (K. Saunders, personal communication), and can serve as a guide for future investigations. Developing habitat suitability indices for Rio Grande silvery minnow in the Big Bend region specifically will be difficult due to the low capture rate.

**Hypothesis 2c: The food web and ecosystem functioning of the river have changed to an alternative state relative to the historic condition**

The altered hydrologic regime may have altered the seasonal cycle of turbidity versus clear water and is now mismatched relative to organism life cycles. In particular, algal food production may be limited during critical growth periods for the silvery minnow. An altered hydrologic regime may also have altered the storage and suspension of organic matter and is resulting in frequent hypoxic events. Another possibility is that changes in the riparian vegetation affect the delivery of allochthonous sources of energy, and the silvery minnow is not adapted to use these unique energy sources.

To investigate the potential for altered turbidity timing to impact the algal food base, current samples could be compared to any available historic data, potentially including cores from Lake Amistad, which would at least preserve a record of diatom composition, a favored food source for the minnow. Cores taken from the mainstem in Big Bend could potentially provide a historical record of benthic organic matter accumulation. Tracking availability of different algal food sources over time would also help answer this question, and simultaneous studies of growth patterns of Rio Grande silvery minnow, including otolith analysis and isotope analysis to determine trophic position and resource use of minnows would further refine whether minnows are limited from using algal food resources during certain times of the year. Currently, analysis of fish diets and comparison to historic specimens, as well as otolith aging is ongoing, and monitoring of algal food resources is planned for future sampling trips (M. Montagne, USFWS, and K. Saunders, TPWD, personal communication). Thus, data should be available soon to help answer these food-web related questions.

The importance of vegetation changes can be assessed by comparing allochthonous resource inputs (e.g., leaf litter and terrestrial invertebrates), in areas dominated by native versus non-native vegetation. Comparing these inputs to silvery minnow diets and isotope
composition would yield further insight on the resources used by silvery minnow in reaches with different vegetation types.

The third potential limiting ecosystem change suggests that small or moderate flood events suspend flocculated organic matter and silt from the bed of the river, stimulating bacterial decomposition and leading to hypoxic conditions and fish kills. One analysis that can be done to look for a link between flood events and hypoxic conditions would be to plot discharge around the time of anoxic events to see if flow peaks before these events. If evidence of a link between flow events and hypoxic conditions is present, further research would need to explore the hydrologic conditions and organic matter inputs that could lead to accumulation of the flocculant/silty layer on the bed. Despite occurrence of short-duration hypoxic events, ecologically similar species to the Rio Grande silvery minnow, such as red shiner and Tamaulipas shiner, have persisted within the region, suggesting these events are not widespread or severe in their impacts. However, the low population of Rio Grande silvery minnow may make them particularly susceptible to even small, isolated disturbance events.

Summary

As binational efforts to manage and restore the Rio Grande ecosystem in the Big Bend region continue, providing scientific information to guide these efforts will be critical. Much work has been done in the region to understand the hydrological, geomorphic, and biotic components of the ecosystem and their driving processes. However, much is still unknown, particularly with regard to the linkages between physical and biotic components and the relative importance of controlling factors in shaping the organization of biotic communities. Thus, we recommend a coordinated effort to collect hydrologic, water quality, geomorphic, and biotic data at a suite of established study sites be developed. Analysis of data collected through a coordinated program with methods such as structural equation modeling (as just one example) can yield important insight into the relative influences of different controlling factors on biotic communities. Specific investigation of factors potentially limiting Rio Grande silvery minnow in a systematic way will help reintroduction efforts and add further understanding to the relative influence of limiting factors. Providing such insight will help guide future management actions, which will be critically important, as future streamflow patterns are expected to shift further due to climate changes and increasing water demand and use in the Rio Grande basin (Porter et al. 2009, Ingolf-Blanco and McKinney 2010).
Figure 12. Flow chart outlining recommended research approach for investigating limiting factors for Rio Grande silvery minnow.
Literature Cited


