

# Reproductive Phenology and Fish Community Structure in an Arid-Land River System

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*Abstract.*—Timing of reproduction differs among fish species in nearly all rivers, and reproductive phenology is predicted to strongly influence freshwater fish community structure in some systems. Despite its potential importance, few long-term studies of reproductive phenology in river fishes have been conducted in a community context. Here, we evaluated timing and sequence of reproduction of fishes in the Rio Grande, New Mexico over 9 years. Dates and rank order of first appearance of larvae varied among species and years, but three consistent spawning guilds were evident: early season, late season, and species that were intermediate in rank order of spawning. We hypothesized that appropriate reproductive timing enhanced recruitment to the extent that spawning cues predicted future availability of critical resources for larvae. Analysis of historical discharge records indicated that present and future discharge exhibited positive autocorrelation for up to 90 d. Likewise, larval fish densities were highest at moderate flows and coincident with high food resource abundance. However, stable isotope data for larval and adult fishes indicated considerable overlap in food resource use among larvae and adult fishes. There may be pressure for spawning time to converge among species to match the appearance of seasonal resources, but to diverge to lessen competition among young-of-year fishes in a classical trade-off scenario. More long-term studies are needed, and we propose that an integrated research program that combines detailed analysis of reproductive phenology, food web dynamics, and comparative genomic analyses could forge connections between environmental variation in spawning cues, recruitment success, and community assembly in river fishes. Such an integrated program could lead to better predictions about fish community responses to global warming, especially in vulnerable arid-land systems like the Rio Grande.

## Introduction

Seasonal variability in spawning time among species is ubiquitous in freshwater fish communities throughout the world (Bye 1984; Peterson and VanderKooy 1995; Matthews 1998; Pusey et al. 2001). In medium to large temperate river systems, there are typically

fishes that spawn during high flows in spring and fishes that spawn during low flows in midsummer through autumn (Ross and Baker 1983; Finger and Stewart 1987; Turner et al. 1994; Humphries et al. 1999; Zeug and Winemiller 2008). As the growing season progresses, there is sequential addition of species to the young-of-the-year (YOY) fish community through recruitment, and loss

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as fishes succumb to predation or starvation, or grow and emigrate from larval nursery grounds. Peak species richness in the YOY community is typically observed when offspring from both reproductive guilds overlap in early summer (Moore and Thorp 2008). Maximal abundance and richness coincide with moderate flows and high habitat heterogeneity because both channel and backwater areas are present in the riverscape. In this way, reproductive phenology affects community composition and the opportunity for biotic interactions among members of the YOY fish community.

Schlosser (1987) hypothesized that reproductive phenology would most strongly affect adult fish community composition in warmwater streams with high variability in discharge, low habitat heterogeneity, and limited refugia from harsh conditions at some stage in the life histories of constituent species. Schlosser's conceptual model could logically be extended to larger arid- and semi-arid catchments because these systems exhibit geomorphic and hydrologic characteristics that should also favor phenological control over YOY and adult fish community structure (e.g., Humphries et al. 1999; Pease et al. 2006; Hoagstrom et al. 2008). In these systems, flow regimes are highly variable with respect to magnitude and duration of flooding and intermittency events, relative to mesic streams of comparable drainage area (Ross et al. 1985; Poff et al. 1997; Puckridge et al. 1998). Inter- and intra-annual variation in flow appears to promote recruitment success of early- (usually high flow) and late-season (usually low flow) spawners, thereby enhancing total species richness by allowing species with early- and late-season reproduction to coexist (Humphries et al. 1999; King et al. 2003; Pease et al. 2006).

If these generalities are correct, then un-

derstanding the ecological and evolutionary forces that determine when different species spawn and how variation in spawning time is maintained is of paramount importance to understanding the assembly of river fish communities. Full understanding requires transcendence of four levels of ecological hierarchy where abiotic conditions (ecosystem properties) stimulate behavioral responses that initiate spawning (individual properties), which in turn affect population and community dynamics through the temporal sequence of recruitment, growth, and species interactions. This general framework raises a number of questions, however. For example, how variable is reproductive phenology among years? Is there a general relationship between early and adult life histories that influence spawning time (e.g., Winemiller and Rose 1992; Fonseca and Cabral 2007; Zeug and Winemiller 2007; Tedesco et al. 2008)? How does reproductive timing coincide with resource availability (e.g., Whitfield 1999)? Do patterns of reproductive phenology offer insight into the extent that among-species differences in spawning time are genetically "hard-wired" and/or modified by environmental conditions (Bye 1984)? Answers to these questions require integrated ecological and genetic research on YOY and adult fish community dynamics, as well as time-series data of sufficient duration to assess whether generalities in reproductive timing and sequence exist. Such long-term data sets have rarely been collected for river fish communities.

Our aim in this paper was to take a first step in describing and developing a program that integrates traditional YOY fish community ecology and comparative study of the environmental and, ultimately, genetic control of reproductive timing differences among species. We addressed the following questions: (1) Does the onset and rank order of species

spawning times differ among years for a 9-year time series in the Rio Grande?, (2) How well does discharge on a given day predict availability of surface water later in the growing season?, (3) How does spawning sequence and larval fish density coincide with resource (surface water, food) availability under different hydrological regimes?, and (4) Do YOY fishes partition food resources among species or among life stages in the Rio Grande? We concluded by evaluating the potential of using comparative ecological genomics to help elucidate differences and similarities in environmental cues that initiate and control spawning in river fishes.

## Methods

### Study Site

This study was conducted in a 280-km river reach (known locally as the “middle Rio Grande”) in

New Mexico, USA. This reach comprises about 8% of the total length of the river and supports a burgeoning human population and extensive irrigated agriculture in the valley. River flows are regulated by dams designed to control flooding and to extract and store water for cities and agriculture (Figure 1). Peak discharge in the system usually coincides with snowmelt in the southern Rocky Mountains, and smaller discharge events are driven by sporadic late summer monsoon rains. Extensive drying and intermittent flows are common in the basin, especially during drought cycles driven in part by El Niño and Pacific Decadal climatic oscillations (Sheppard et al. 2002). Seasonal floods, drying, and intermittency were prominent parts of the historical context under which the Rio Grande fish community evolved. However, river regulation over the past century has diminished the magnitude, duration, and extent of seasonal floods and increased the duration and extent of river inter-

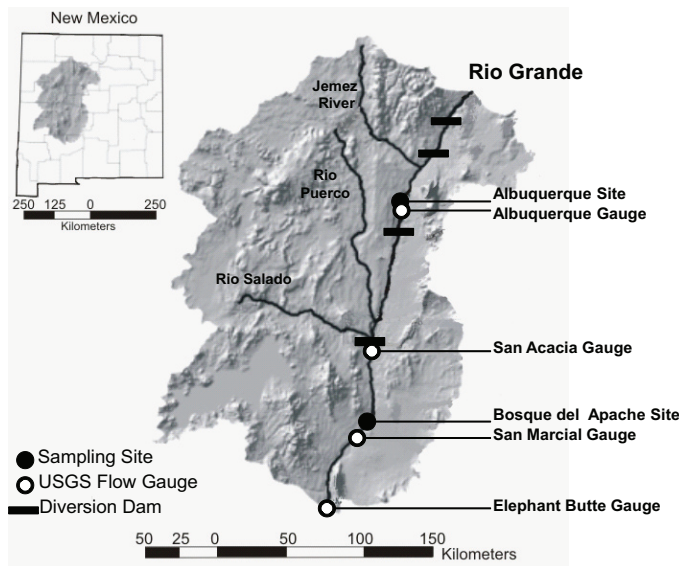


Figure 1. Study reach in the middle Rio Grande, New Mexico. Cochiti Dam and gauge is the furthest upstream (and northernmost) site pictured and Elephant Butte Dam and gauge is downstream-most (no larvae were sampled from Elephant Butte Reservoir). Embudo and Otowi Bridge gauges are upstream of the study area. Larval light trapping was conducted at the Albuquerque site in 1995 and at the Bosque del Apache site in 2003. Instream productivity studies were conducted in 2006 and 2007 at Bosque del Apache. Larval seine surveys were conducted at more than 16 sites within this reach between 1996 and 2007.

mittency events on an annual and interannual basis (Molles et al. 1998).

### *The Fish Community*

The middle Rio Grande fish community is dominated by members of the freshwater families Cyprinidae (minnows) and Catostomidae (suckers) in species richness and numerical abundance (Platania 1991). Native cyprinids in the system are generally short-lived (5 years or less) and capable of completing their life histories in 1 or 2 years (Table 1), which together suggest rapid growth of YOY fishes, high adult mortality rates, and recruitment-driven demography. White sucker *Catostomus commersonii* and common carp *Cyprinus carpio* are two of the largest (and longest-lived) fishes in the reach, and both are introduced. Another introduced species, channel catfish *Ictalurus punctatus*, is also long-lived (and large-bodied) but exhibits nest guarding and larger eggs and hence greater energetic investment per offspring (Stearns 1992). The live-bearer western mosquitofish *Gambusia affinis* is thought to have been introduced into the middle Rio Grande (Platania 1991), although the species is native in downstream reaches. We adopted the triangular life history strategy scheme of Winemiller and Rose (1992) to describe suites of adult life history characters and their relationship to the expected onset and duration of spawning (Zeug and Winemiller 2007, 2008; Tedesco et al. 2008). We also compiled (largely anecdotal) information about exogenous cues that purportedly induce or are at least correlated to the onset of spawning (Table 1 and references therein).

### *Young-of-Year Fish Data*

To study reproductive phenology over a time series, we compiled information on the date of first appearance of larval fishes from three studies that together encompassed 9 (non-

consecutive) years of YOY fish surveys in the middle Rio Grande. In the first data set, sampling was conducted each year on a quarterly or monthly basis with a fine-mesh larval fish seine as part of a monitoring study of the Rio Grande fish community at 16 sites distributed across the study reach (S. P. Platania and R. K. Dudley, Museum of Southwestern Biology, unpublished). Young-of-year fish data for 1995 and 2003 were obtained from geographically localized but more temporally frequent sampling via quatrefoil larval light traps deployed twice weekly from April to September 1995 at the North Diversion channel inlet in Rio Grande near Albuquerque (data provided by S. P. Platania) and weekly from April to July 2003 at the Bosque del Apache National Wildlife Refuge downstream of Albuquerque (Pease et al. 2006). Because sampling gear, geographic scope, and temporal frequency of sampling differed across years, we chose the date of first appearance of larvae as an indicator of the onset of reproduction for that species in a particular year. We did not attempt to back-calculate to the time of spawning from the size or appearance of larval specimens. Ten species were ranked by date of first appearance for each year with ties allowed (Table 2).

We tabulated average ranks for each species across years and calculated upper and lower bound 95% comparison intervals using a Monte Carlo simulation approach. For each species, ranks were resampled (with replacement) across years 9,999 times, creating a set of pseudo-replicates. The mean was calculated for each pseudo-replicate and then plotted to create frequency distribution of mean ranks for each species. The lower bound of the comparison interval was equal to observation 250, and the upper bound equal to observation 9,750 in the cumulative frequency distribution. Two species were deemed significantly different in rank order if their comparison intervals did not overlap.

Table 1. Life history and spawning characteristics of common Rio Grande fishes captured as larvae in this study. Data were compiled from species descriptions in Sublette et al. (1990) unless otherwise indicated by superscripts. Spawning strategy is based on the scheme of Winemiller and Rose (1992). Abbrev. = abbreviation of species name used throughout the paper, Max size = maximum size reported in Sublette et al (1990), age mat = age of maturation for females in years, fecundity = maximum number of eggs or offspring (*Gambusia*) counted per female, native? = native to the study reach. TL = total length.

| Species   | Abbrev. | Max size (TL, mm) | Age mat (♀) | Fecundity | Native? | Spawning strategy | Spawning cues                        |
|---|---------|-------------------|-------------|-----------|---------|-------------------|--------------------------------------|
| White sucker<br><i>Catostomus commersonii</i>                       | Cat_com | 350               | 3, 4        | 59000     | no      | Periodic          | Photoperiod, discharge               |
| Common carp <sup>a</sup><br><i>Cyprinus carpio</i>                  | Cyp_car | 500               | 3, 4        | 220000    | no      | Periodic          | Photoperiod, inundation, temperature |
| Rio Grande silvery minnow<br><i>Hypognathus amarus</i> <sup>b</sup> | Hyb_ama | 90                | 1           | 3000      | yes     | Periodic          | Discharge                            |
| Fathead minnow<br><i>Pimephales promelas</i>                        | Pim_pro | 60                | 1           | 12000     | yes     | Equilibrium       | Photoperiod, temperature             |
| River carpsucker<br><i>Carpiodes carpio</i>                         | Car_car | 350               | 3           | 105000    | yes     | Opportunistic     | Temperature                          |
| Flathead chub<br><i>Platygobio gracilis</i> <sup>c</sup>            | Pla_gra | 145               | 2           | 4000      | yes     | Opportunistic     | Discharge, temperature               |
| Longnose dace<br><i>Rhinichthys cataractae</i>                      | Rhi_cat | 100               | 2           | 10000     | yes     | Opportunistic     | Discharge, temperature               |
| Western mosquitofish <sup>d,e</sup>                                 | Gam_aff | 50                | 1           | 1308      | no      | Opportunistic     | Photoperiod                          |
| Red shiner<br><i>Cyprinella lutrensis</i> <sup>f</sup>              | Cyp_lut | 75                | 1           | 580       | yes     | Opportunistic     | Photoperiod, conspecifics            |
| Channel catfish <sup>g</sup><br><i>Ictalurus punctatus</i>          | Ict_pun | 1,300             | 2, 3        | 52000     | no      | Equilibrium       | Photoperiod, temperature             |

<sup>a</sup> McPhee 2007; <sup>b</sup> Platania and Altenbach 1998; <sup>c</sup> Iwerks and colleagues, Museum of Southwestern Biology, unpublished; <sup>d</sup> Haynes and Cashner 1995; <sup>e</sup> Platania 1991; <sup>f</sup> Asbury et al. 1981; <sup>g</sup> Tyus and Nikirk 1990.

### Surface Water Resource Availability

Spring runoff coincides with spawning in some Rio Grande fishes (Platania and Altenbach 1998; Dudley and Platania 2007), so we were interested in assessing the extent to which discharge on any given day was correlated to discharge later in the growing season. To do this, we first obtained river discharge data (m<sup>3</sup>/s) from the U.S. Geological Service (USGS) flow gauges (<http://waterdata.usgs.gov>) at six locations, listed here from upstream to downstream: Embudo (USGS 08279500), Otowi Bridge (USGS 08313000), Cochiti (USGS 08330000, USGS 08317400), Albuquerque (USGS 08330000), San Marcial (USGS 08358500, 08358400), and Elephant Butte (USGS 08361000) just below the dam. At Cochiti, the flow gauge was moved downstream

of the dam site prior to construction of Cochiti Dam in 1973, and data from the two gauges listed for that site were combined. At San Marcial, the Rio Grande at San Marcial gauge (USGS 08358500) was used for discharge data for 1899–1964, and Floodway at San Marcial gauge (USGS 08358400) was used for 1965–2007. From these data, we calculated autocorrelation functions for daily historical flow data for each gauge. These functions measure the Pearson correlation coefficients between each daily discharge value and a future discharge value after a given lag time measured in days.

### Evaluation of Food Resource Availability and Use

Surveys of environmental variables, instream algal biomass, and densities of invertebrates and

Table 2. Ranks (including ties) of first appearance of larvae over nine growing seasons in the Middle Rio Grande, New Mexico. In each year, sampling began in April and concluded in August (or September in 1995). Two gear types (larval seine and quatrefoil larval light traps) were used to obtain larval fishes. Sampling frequency differed among years from biweekly to quarterly. Species abbreviations follow Table 1. Light-trap survey data from 1995 were provided by S. Platania; other light trap data were obtained from Pease et al. (2006), and larval seine data were provided by Platania and Dudley (unpublished).

| Year         | Gear type    | Frequency | Rank first appearance of larvae by species |             |                           |                |                  |               |               |                      |            |                 |
|--------------|--------------|-----------|--|-------------|---------------------------|----------------|------------------|---------------|---------------|----------------------|------------|-----------------|
|              |              |           | White sucker                               | Common carp | Rio Grande silvery minnow | Fathead minnow | River carpsucker | Flathead chub | Longnose dace | Western mosquitofish | Red shiner | Channel catfish |
| 1995         | Light trap   | biweekly  | 1  | 2           | 3                         | 4              | 6                | 5             | 8             | 8                    | 7          | -               |
| 1996         | Larval seine | quarterly | 1  | 1           | 1                         | 1              | 1                | 1             | 1             | 2                    | 3          | 2               |
| 2000         | Larval seine | quarterly | 1  | 2           | 3                         | 2              | 2                | 3             | 2             | 2                    | 2          | 4               |
| 2002         | Larval seine | monthly   | 1  | 2           | 2                         | 2              | 1                | 2             | 2             | 2                    | 3          | -               |
| 2003         | Light trap   | weekly    | 1  | 2           | 4                         | 3              | 4                | -             | -             | 4                    | 5          | -               |
| 2004         | Larval seine | monthly   | 1  | 1           | 1                         | 1              | 1                | 1             | 2             | 1                    | 2          | 3               |
| 2005         | Larval seine | monthly   | 2  | 1           | 1                         | 1              | 1                | 4             | 3             | 2                    | 3          | 5               |
| 2006         | Larval seine | monthly   | 1  | 1           | 1                         | 1              | 1                | 2             | 2             | 1                    | 2          | 3               |
| 2007         | Larval seine | monthly   | 1  | 3           | 3                         | 4              | 2                | 3             | 1             | 3                    | 4          | 5               |
| Rank average |              |           | 1.11                                       | 1.67        | 2.11                      | 2.11           | 2.11             | 2.63          | 2.63          | 2.78                 | 3.44       | 3.67            |
| Rank SD      |              |           | 0.33                                       | 0.71        | 1.17                      | 1.27           | 1.76             | 1.41          | 2.26          | 1.67                 | 1.21       | 2.17            |

fishes were conducted weekly in summers of 2006 and 2007 at Bosque del Apache National Wildlife Refuge (Figure 1). At least three samples were taken each week, but exact sampling localities differed across weeks because these habitats were ephemeral during the growing season. Environmental data included sample date (Julian day), daily river discharge at the USGS San Acacia gauge (USGS 08354900), length and width of the sample area (m), and depth of water (cm). Physicochemical variables measured were water temperature ( $^{\circ}\text{C}$ ), dissolved oxygen (mg/L), specific conductivity ( $\mu\text{S}/\text{cm}$ ), salinity (parts per thousand), and turbidity.

At each distinct sample site, sediment cores were collected from shallow (<3 cm deep), medium (3–10 cm deep), and deep (>10 cm) points with a modified syringe (diameter = 2.6 cm; 2 mm deep). In the laboratory, these three samples were combined and extracted with ethanol (95%). Chlorophyll-*a* concentration ( $\text{mg}/\text{m}^2$ ) was estimated by measuring optical densities of extracted samples with an HP 8452A diode array spectrophotometer (Sartory and Grobbelaar 1984). Invertebrates and fishes were quantitatively sampled using a 0.25- $\text{m}^2$  throw trap (see Turner and Trexler 1997 for sampling properties of the throw trap). After placement, the throw trap was pushed into the top layer of sediment to seal off a section of the water column. Three types of gear were employed for subsampling within the trap. For water column (pelagic) sampling, a polyvinyl chloride tube (length = 30 cm, diameter = 7.5 cm) was held horizontally and immersed approximately 10 cm below the water surface, and the ends sealed. Epibenthic core samples were collected as described in King (2004). Larger invertebrates and fishes were collected by passing a 500- $\mu\text{m}$  mesh dip net through the throw trap until returns were diminishing.

For all gear types, contents were passed through a sieve (47  $\mu\text{m}$  mesh), stored in 70% ethanol, and then transported to the laboratory for identification and processing. Aquatic organisms were identified to the lowest practical taxonomic level; generally, microcrustacea were identified to order, insects were identified to family, and fishes were identified to species using published and unpublished keys (e.g., Merritt and Cummins 1996; Smith 2001; Thorp and Covich 2001; W. H. Brandenburg, Museum of Southwestern Biology, personal communication). Temporal patterns of resource availability were evaluated by plotting primary (chlorophyll-*a* concentration) and secondary (densities of invertebrates and fishes) standing stocks by time in weeks. We summarized relative abundances of the larval fishes for 2006 and 2007 and used rarefaction to compute and compare species richness and Shannon's diversity index between years.

To evaluate larval and adult fish resource use, we reanalyzed previously collected stable isotope data sets for Rio Grande fish larvae (Pease et al. 2006), primary producers, invertebrate consumers, and adult fishes (Edwards 2006). Stable isotope ratios of carbon and nitrogen were determined by mass spectrometry and are reported in delta notation ( $\delta^{13}\text{C}$ ;  $\delta^{15}\text{N}$ ), as described in the references above. Delta values of all samples were plotted to place productivity and larval and adult fish resource use data into context within the river food web. We quantitatively examined overlap in isotopic values between larval ( $n = 55$ ) and adult fishes ( $n = 22$ ), with species pooled within each group to increase sample sizes. First, we computed group centroids in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  biplot space for larval and adult fishes, respectively. We then computed mean Euclidean distance of individual delta values to the group centroid (CD) and the mean Euclidean distance to each individual observation's nearest neigh-

bor (NND). These metrics summarize location, dispersion, and “clumping” of individual delta values in bivariate ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) space, as described in Layman et al. 2007, and provide a means to test for food resource partitioning or overlap among groups.

We tested the null hypothesis that group centroid locations did not differ among larval and adult fishes by computing the Euclidean distance between observed centroids and then, for 9999, randomly permuted pseudo-replicates via a residual randomization procedure. The rank percentile of observed difference between groups was used as an empirical *P*-value for the test of the null hypothesis. We used a similar approach to test the null hypothesis that CD and NND did not differ between larval and adult groups. Finally, we plotted larval fish on a separate graph to qualitatively evaluate the extent of overlap in bivariate isotope space. Larval sample sizes were small ( $n = 11$  per species, on average) and precluded detailed statistical analysis.

## Results

### Spawning Time Variation

Dates of first appearance of larvae varied considerably among sample years and species (Figure 2A). For example, earliest first appearance of any larvae was 23 April 2003 (white sucker) in 2003, a year characterized by low discharge and poor spring runoff (maximum discharge was  $36 \text{ m}^3/\text{s}$  on 16 May 2003). Latest first appearance of any species was 2 August 2000 (channel catfish), which was also a low discharge year (peak discharge was  $42 \text{ m}^3/\text{s}$  on 15 June 2000) with poor spring snowmelt and monsoon runoff. Comparison of mean ranks among species (Figure 2B) indicated three distinct spawning groups based on first appearance of larvae: (1) a group that appeared early (limb of the spring flood pulse), consist-

ing of white sucker and common carp; (2) an intermediate group (descending limb of the spring flood pulse), consisting of Rio Grande silvery minnow *Hybognathus amarus*, river carpsucker *Carpionodes carpio*, fathead minnow *Pimephales promelas*, flathead chub *Platygobio gracilis*, longnose dace *Rhinichthys cataractae*, and western mosquitofish; and (3) a late appearance (summer base flows) group consisting of red shiner *Cyprinella lutrensis* and channel catfish. Comparison intervals computed via Monte Carlo resampling indicated that mean ranks of early-spawning species did not overlap with mean ranks with the late spawning group (Figure 2B). Conversely, there was substantial overlap of ranks in the intermediate group. Despite this, there was a trend suggesting that Rio Grande silvery minnow, fathead minnow, and river carpsucker appeared earlier than longnose dace, flathead chub, and western mosquitofish. Standard deviation of rank appearance was higher for common carp, longnose dace, and western mosquitofish than for Rio Grande silvery minnow, fathead minnow, and flathead chub (Table 2).

### Autocorrelation Analysis of Rio Grande Discharge Patterns

Analysis of daily flow data from six Rio Grande gauges indicated significant and positive autocorrelation of present discharge and future discharge with a lag time of 70–90 d (Figure 3). Pearson autocorrelation coefficients were not significantly different from zero after approximately 90-d lag time for all gauges except for San Marcial, which showed slight but positive autocorrelation that extended for the entire year (Figure 3). At the five other gauges studied, present and future discharge were significantly and negatively (but with small *r*-values) autocorrelated for the period between 100 to about 270 d, and then positively autocorrelated again after 300 d

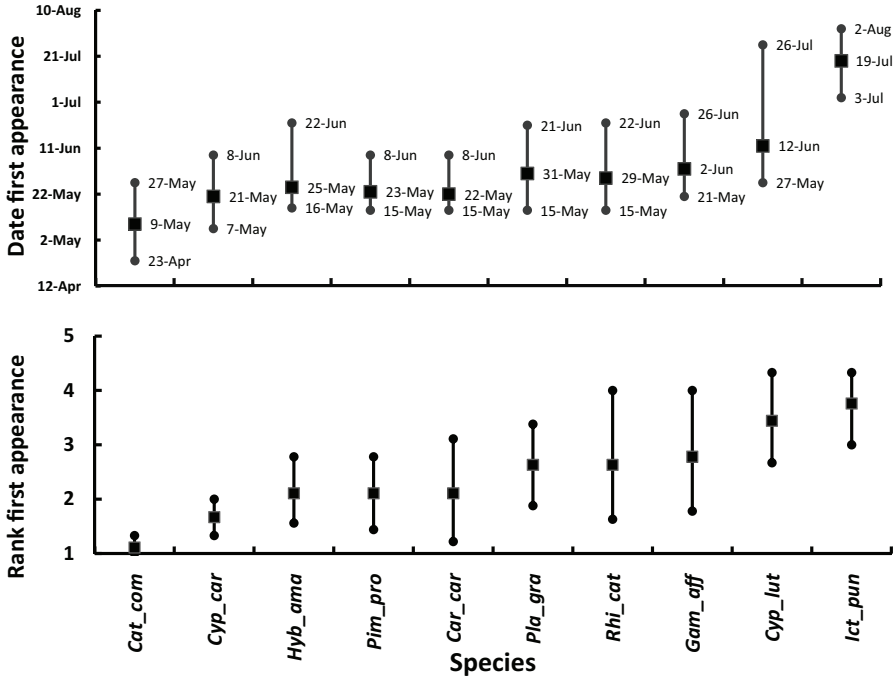


Figure 2. (A) Median dates of first appearance of young-of-year fishes obtained over 9 years of sampling. Bars reflect the range of dates of first appearance for each species. (B) Average rank order of appearance computed over 9 years of sampling and tabulated by species. Bars reflect 95% comparison intervals for mean ranks. Early (*Catostomus*, *Cyprinus*) and late (*Cyprinella*, *Ictalurus*) spawners differed significantly, as comparison intervals do not overlap.

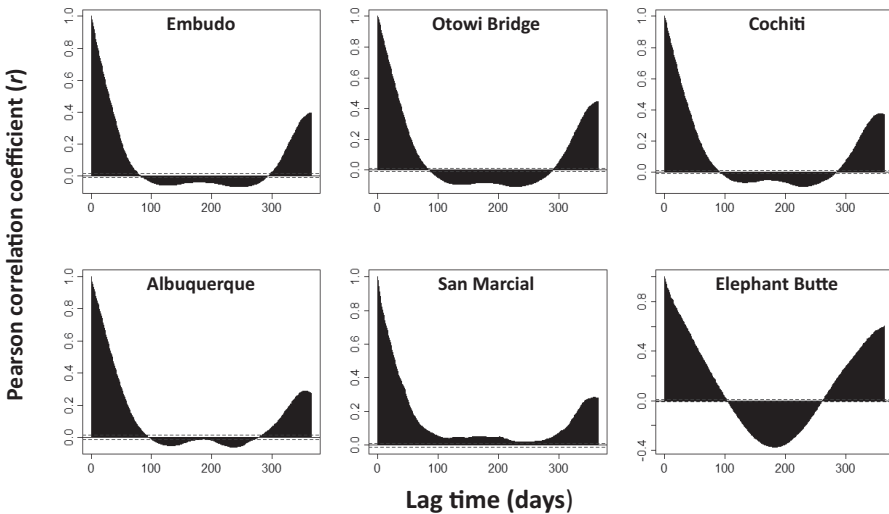


Figure 3. Autocorrelation functions for daily discharge data plotted for six U.S. Geological Survey gauges on the Rio Grande. Plots depict Pearson correlation coefficients ( $y$ -axis) as a function of lag time ( $x$ -axis), measured in days. Note that for all six gauges, flows are positively autocorrelated over a period of up to approximately 90 d, illustrating that current discharge predicts future discharge, even in the highly fluctuating Rio Grande.

(Figure 3). Present and future flows exhibited moderate negative autocorrelation ( $r = -0.35$ ) for the gauge below Elephant Butte Dam at day 190 (Figure 3).

*Temporal Dynamics of Food Resources*

River discharge was related to changes in standing stocks of primary producers and primary consumers in 2006 and 2007, as revealed by throw-trap sampling. Hydrographs in 2006 and 2007 were essentially mirror images of one another; 2006 was characterized by weak spring

runoff (and low discharge) followed by record monsoon precipitation (and high discharge), whereas 2007 exhibited moderate spring flows followed by a weak monsoon (Figure 4). Discharge and turbidity were strongly and positively correlated ( $r = 0.53, P < 0.001$ ). Biomass of chlorophyll *a* and turbidity were negatively correlated ( $r = -0.217, P = 0.018$ ), and invertebrate density was negatively correlated to both discharge ( $r = -0.241, P = 0.018$ ) and turbidity ( $r = -0.319, P = 0.005$ ). Larval fish density was only marginally negatively correlated to discharge ( $r = -0.209, P = 0.040$ ). On aver-

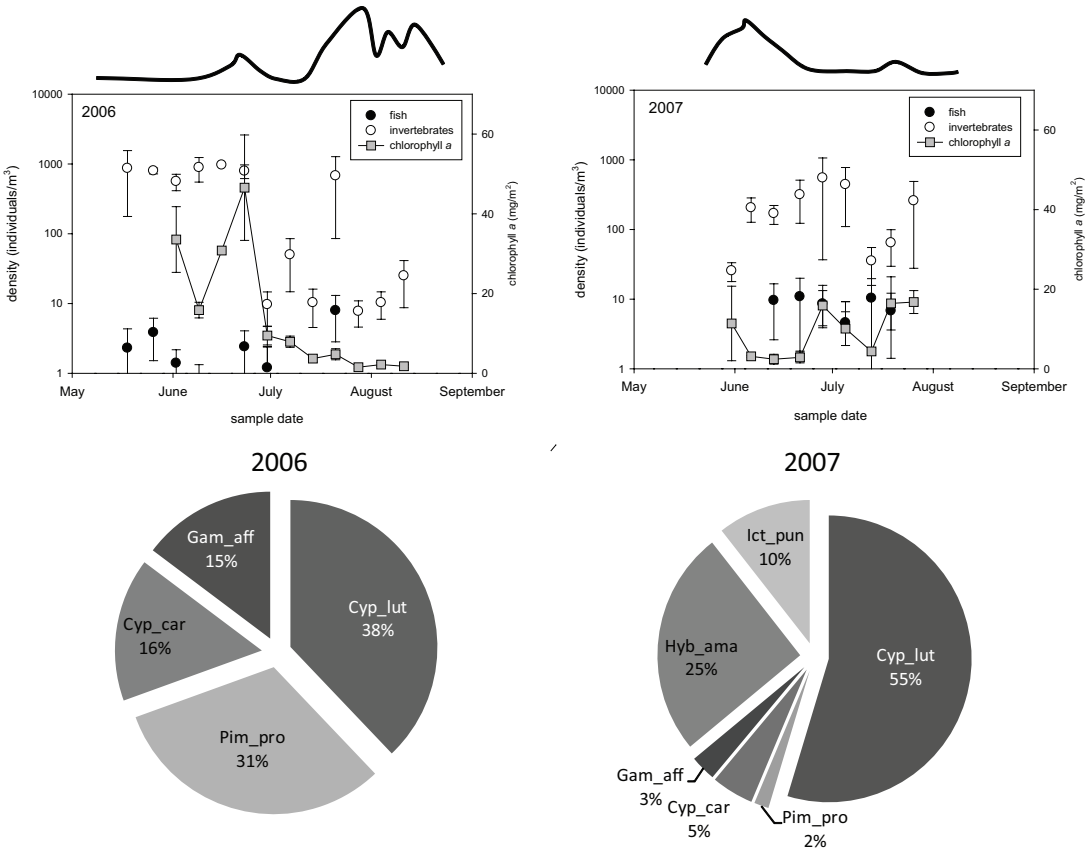


Figure 4. Hydrograph, primary and secondary productivity, and young-of-year (YOY) fish community structure at Bosque del Apache in 2006 and 2007. The top panel is a stylized representation of the hydrographs in 2006 and 2007. The middle panel represents biomass of primary producers (measured as mg/m<sup>2</sup> chlorophyll *a*) and consumers (measured as densities of organisms) plotted by time. Note the log scale on y-axis for densities of invertebrates and fishes but not for primary producers. Relative abundances of YOY fishes for the entire survey season are reported in the bottom panel.

age, larval fish density was five times higher in 2007 than 2006 (Figure 4). Larval fish species richness (after rarefaction) was higher in 2007 (richness in 2007 = 6;  $n = 498$  larvae; richness in 2006 = 4,  $n = 103$  larvae), but evenness was not (Shannon's equitability index for 2007 = 0.70 and 2006 = 0.94). In general, larval fish densities were highest during periods of moderate flows that followed spring runoff or monsoonal rains (Figure 4).

Stable isotope analysis revealed that dietary carbon for larval and adult fishes was obtained predominately from instream (autochthonous) rather than riparian (allochthonous) production, as demonstrated by relatively enriched  $\delta^{13}\text{C}$  values for both groups of fishes (Figure 5). Adults were enriched by approximately 1.98‰ at  $\delta^{15}\text{N}$  relative to larvae, which suggests that adults feed at a slightly higher trophic level (Figure 5) and suggests the pos-

sibility that adults may include larval fishes in their diets on occasion. However, permutation testing revealed that centroid distance (Euclidean distance between larval and adult group centroids) was not significantly different from zero ( $P = 0.575$ ). Likewise, dispersion (as measured by CD) and the degree of "clumping" (as measured by NND) did not differ significantly between groups ( $P$ -value for difference of CD among groups = 0.6528,  $P$ -value for difference of NND = 0.137). Qualitative comparison of larvae from the five most common Rio Grande fishes also revealed considerable overlap in distributions of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values (Figure 6).

## Discussion

If we assume that adult fishes optimize spawning time to maximize offspring survivorship (Stearns 1992; De Camino-Beck and Lewis

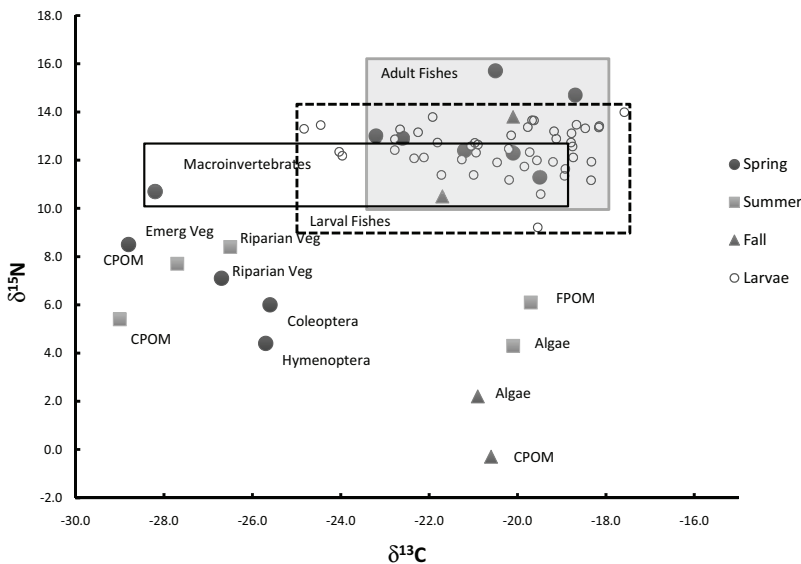


Figure 5. Food web structure at Bosque del Apache (2002–2003) based on signatures of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotopes. Carbon from instream primary producers (algae, emergent vegetation, riparian vegetation, submerged macrophytes, coarse and fine particulate organic matter [CPOM and FPOM, respectively]) fuels the majority of fish production in the river food web (Edwards 2006; Pease et al. 2006). The food web has roughly three trophic levels (primary producers, primary macroinvertebrate consumers, and secondary fish consumers). Larvae are and adults feed at a similar trophic level based on statistical comparison of group centroid locations and dispersion statistics.

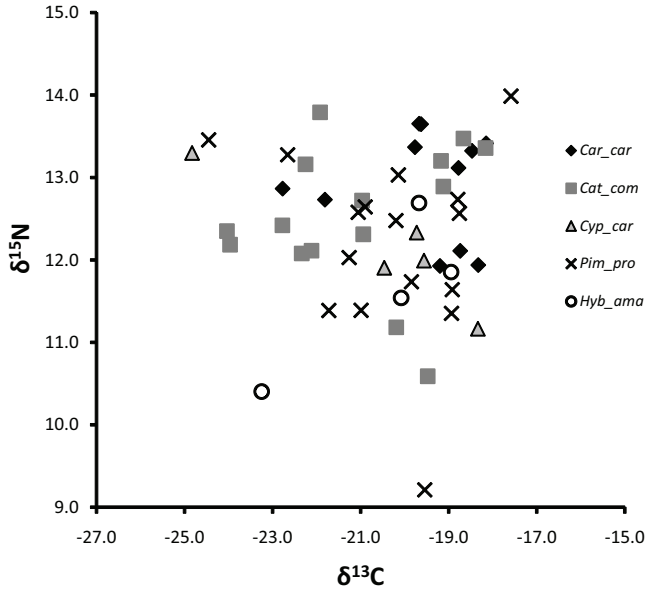


Figure 6. Stable isotope signatures of five species of larval fishes at Bosque del Apache in 2002 (from Pease et al. 2006). Considerable overlap of larval fish stable isotope ratios across species suggested similarity in food resource use.

2008), then, at minimum, spawning activity must match the seasonal timing of critical resources in the environment. We would also predict that if resource requirements for developing larvae were the same for all species, then reproductive timing would be invariant among species. However, if we can reject invariance of spawning time, then alternative hypotheses would be as follows: (1) species in a highly variable system match reproductive activity to shifting environmental conditions, (2) species have different resource requirements and match spawning to temporal appearance of a specific resource, and (3) species diverge in spawning time to minimize risks of competition or predation. These alternatives are neither exhaustive nor mutually exclusive but provide a starting point for discussion of our observation that spawning time varies among species and years in the Rio Grande.

Does spawning time differ consistently among species? Based on a 9-year time series, we found that the date of first larval appearance

differed among years and among species with earliest appearance of first larvae (of any species) in April and latest appearance of first larvae in May. Despite variation in first appearance date, rank orders of spawning were somewhat consistent across years. Comparison of mean ranks among species indicated three groups of spawners: an early spawning group (*Catostomus*, *Cyprinus*) where larvae appeared on the ascending limb of the seasonal hydrograph, an intermediate group where larvae appeared after peak discharge in spring (*Hybognathus*, *Pimephales*, *Carpiodes*, *Platygobio*, *Rhinichthys*, *Gambusia*), and a late spawning group (*Cyprinella*, *Ictalurus*) that appeared during lower flows in summer. Interestingly, nonnative species (*Catostomus*, *Cyprinus*, and *Ictalurus*) were at the temporal extremes (earliest and latest spawners) while spawning in native species were more closely spaced (and intermediate) in time, except for *Cyprinella*. Failure to discriminate ranks of native species stems, probably in part from coarse temporal sampling in most

study years. However, there are some biological differences between natives and nonnatives that may also influence the temporal sequence of spawning. Reproductive timing of nonnatives evolved outside the Rio Grande system, and so their appearance at temporal extremes may be vestigial. However, to persist in the Rio Grande, nonnatives must produce offspring at least once in their lifetime. Common nonnatives are generally longer-lived than natives in the system and therefore have the opportunity to reproduce many times over their life spans, which may assure successful reproduction at least once. Natives may converge on spawning time because they are (generally) shorter-lived and have less tolerance for recruitment failure in any given season, simply because they have fewer opportunities for future reproduction over their short lives.

Although ranks of the intermediate group did not differ significantly from one another based on 95% comparison intervals, there was an apparent trend in temporal sequence of appearance of larvae of these species. *Hybognathus* and *Pimephales* spawned earliest on average, followed by *Platygobio* and *Rhinichthys* and then by *Cyprinella*. *Cyprinella* spawned significantly later than early (nonnative) spawners, had the most variable date of first appearance, and achieved very high abundances as larvae late in the growing season in 2006 and 2007 (see also Pease et al. 2006). In the Rio Grande, native species appear to employ two distinct strategies, either to tightly match and synchronize spawning time to the availability of key resources (e.g., *Hybognathus*) or to have a bet-hedging strategy (e.g., *Cyprinella*) that allows recruitment success in the face of highly variable environmental conditions (Stearns 1992).

Our results are consistent with a number of studies of fish reproductive phenology conducted over shorter time spans (Marchetti and

Moyle 2000; Zeug and Winemiller 2008), and together they allow formation of several postulates about the nature of environmental and genetic control over spawning time. In general, freshwater fishes are plastic in timing of key events of the life history, presumably to surmount dramatic fluctuations in environmental conditions (Reebs 2002). A corollary to this idea is that fishes in stochastically variable and potentially harsh environments should exhibit more intraspecific variation in spawning time than those in more benign environments, all else being equal (Zeug and Winemiller 2008). Thus, a key determinant of reproductive success and specific timing of spawning of any species depends on how well current conditions predict future conditions.

How well does current discharge predict availability of surface water later in the growing season? In order to match the appearance of resources in the environment, spawning must be initiated by cues that give some information about future conditions. Of the putative abiotic spawning cues identified in Table 1, photoperiod is a strict determinant of seasonal timing, but temperature and discharge are much less so, at least in the Rio Grande. Accordingly, day length is almost universally used by organisms to time key life history events like reproduction, growth, and migration in temperate environments (Bradshaw and Holzapfel 2008), including fishes (Bye 1984; Ahas and Aasa 2006). However, if photoperiod was the only determinant of spawning time in Rio Grande fishes, then the onset of spawning and first appearance of larvae should occur at the same time each year, which was not observed. Rather, photoperiod likely plays a role in reproductive readiness (i.e., gonadal recrudescence) while temperature and/or discharge are proximal cues for initiating spawning (Stacey 1984).

One might expect that in a temperate system with stable flows, coupled photoperiod,

and temperature regulation of spawning time would virtually guarantee appropriate matching of spawning and resources if food was the only limiting resource (e.g., DeHaven et al. 1992). In arid-land systems such as the Rio Grande, surface water is also critically limiting. Such extensive variability in water availability throughout the growing season begs the question of whether key discharge events (like peak flows in springtime) give any information about water resource availability later in the growing season (e.g., Pusey et al. 2001).

Pearson autocorrelation analyses indicated that discharge patterns were autocorrelated for a lag time of up to 90 d, indicating that both high (and low) discharge events contain information about future water availability in the Rio Grande over the critical period of early development. Interestingly, moderate negative autocorrelation was observed at gauges that were immediately below reservoirs like Cochiti and, to a greater extent, Elephant Butte. The operations of these facilities may change autocorrelation patterns and thus the information content that present discharge has about future discharge (e.g., Bunn and Arthington 2002).

How does spawning sequence and larval fish density coincide with resource availability (surface water, food) under different hydrological regimes? There appear to be fitness consequences for fishes that cue spawning on spring discharge events when there is a poor spring flood pulse in the Rio Grande. Throw-trap sampling revealed that the endemic and federally endangered Rio Grande silvery minnow exhibited very poor recruitment in 2006 (where no spring flood pulse occurred) but comprised the bulk of the spring larval fish assemblage in 2007 (a year characterized by a strong spring flood pulse). In 2006, the spring assemblage of larval fishes was dominated by fathead minnow, a nesting minnow that requires low flows

to successfully construct nests, attract mates, and defend territories (Sublette et al. 1990).

Throw-trap data also indicated that standing stocks of primary producers and consumers were highest (per unit area) in early summer 2006, a year that was characterized by extremely low flows in spring time. Wetted surface area was also limited during this time, and the river was reduced to a number of small pools. Primary producers (mainly algae) responded positively to increased light penetration in relatively clear pools, so standing stocks reflect local production. Densities of invertebrates probably increased because of in situ production and the concentration of existing organisms into smaller wetted habitat. Standing stocks of both chlorophyll *a* and invertebrates were lowest during periods of high discharge in late summer 2006 and during high flows of early summer 2007. Despite variability in food resource availability (especially micro- and macroinvertebrates), average densities of larval fishes were consistent across weeks within years, suggesting sufficient resources to support some larvae throughout the growing season. Larval fish densities were roughly five times higher in 2007 than in 2006.

Do YOY fishes partition food resources among species or among life stages in the Rio Grande? Stable isotope analysis revealed considerable potential for overlap in resource use among larval fishes and between larvae and adults at the Bosque del Apache site in the Rio Grande. There are probably important limitations in discriminatory power to resolve resource differences using stable isotopes alone (Layman et al. 2007), so our observations and conclusions below are tentative. First, most of the carbon fuelling the river food web was derived from instream (algal) production rather than terrestrial input, which is similar to other arid-land rivers (Bunn et al. 2003). Second, there was little heterogeneity evident in basal

energy sources for larvae or adults. In general, adults and larvae of all species had broadly overlapping stable isotope signatures, suggesting that they use the same or very similar food resources. Of course, any definitive argument regarding the role of competition in maintenance of spawning time will require demonstration of limitation of food resources in the system. Although not statistically significant, adults exhibited enriched  $\delta^{15}\text{N}$  values relative to larvae, a result that indicates that adults may feed on larvae occasionally but not predominately. Overall, our analyses suggest that spawning time differences among species may be maintained to minimize negative biotic interactions (competition predominately) and to maximize coincidence with species-specific resources (e.g., nesting sites in *Pimephales*).

#### *Reproductive Phenology and Fish Community Composition in the Rio Grande*

Environmental variation has long been recognized as a primary driver of fish community structure in temperate freshwater streams and rivers (Grossman et al. 1982; Schlosser 1987), and it is especially important where harsh conditions predominate (Ross et al. 1985). The Rio Grande experiences both predictable and stochastic fluctuations in environmental conditions that are sometimes harsh and are likely to have strong effects on fish community structure. Springtime flooding is usually predictable, benign, or perhaps even beneficial to some fishes because floods expand laterally and increase habitat size. Severe drying events in summer and early autumn are less predictable and negatively impact fishes by decreasing habitat and increasing intensity of negative biotic interactions (i.e., a competitive crunch, Wiens 1977). In summer and early autumn, the Rio Grande fish community is dominated by YOY individuals, suggesting that important

interactions of abiotic factors, biotic factors, and fish community structuring are most likely to occur during early life history stages.

Although not definitive, our results support the idea that temporal dynamics of reproduction, hydrological variability, and their interactions are likely to be primary determinants of fish community structure in the Rio Grande. There is a consistent interspecific sequence of spawning time that relates to reproductive life history (periodic spawners early, opportunistic, and equilibrium either intermediate or late) and considerable intraspecific variation in spawning time that appears to depend strongly on the timing and magnitude of abiotic cues predominately related to temperature and discharge. More frequent temporal sampling over multiple years will be required to fully resolve spawning time variation among native Rio Grande fishes. Differences in spawning time among species are probably maintained by a combination of biotic (competition and, to a lesser extent, predation) and abiotic factors related to species-specific resource needs.

#### *Future Research*

If annual and seasonal hydrological variability and temperature play critical roles in structuring the fish community in the Rio Grande, then comparative ecological study of spawning time has enormous potential to reveal important information about genetic control of spawning initiation in river fishes. For species that cue spawning on discharge, for example, it would be of great interest to predict how alterations in timing, magnitude, and duration of flows affect spawning success. Native cyprinids in the Rio Grande, coupled with genomic information on an evolutionarily related model species (zebra danio *Danio rerio*), offer the exciting potential to understand the mechanics of spawning induction, the scope for plasticity in the spawn-

ing response, and the degree of similarity of spawning responses across species.

There has been considerable work on the genetic pathways associated with photoperiod and temperature perception in *Danio*; namely, two gene families (clock and period) have been shown to control organism response to day-length changes (Lahiri et al. 2005). Interestingly, period-4 is downregulated under low temperature conditions, suggesting the intriguing possibility that organism responses to photoperiod and temperature are co-regulated by these gene families (Lahiri et al. 2005) and that initiation of spawning could be cued through this co-regulatory pathway. It would be interesting to evaluate expression patterns of these genes in a community context among cyprinids in the Rio Grande using the *Danio* system as a model pathway. For example, we would predict differential expression in these genes between early (e.g., *Hybognathus* and *Pimephales*) and late-season (e.g., *Cyprinella*) spawners.

We recently concluded an experiment that evaluated the efficacy of microarray technology for gene discovery (sensu Wang et al. 2008) in Rio Grande cyprinids. Preliminary results indicated that the vast majority of 22,000 expressed genes in *Pimephales* are expressed similarly in *Hybognathus* (T. J. Krabbenhoft and T.

F. Turner, unpublished). These results suggest that microarray technology, or, alternatively, next-generation DNA sequencing, could be used in a comparative context to discover genes that are up- or down-regulated in the presence of absence of abiotic spawning cues, which could potentially lead to a better understanding of key spawning cues. Table 3 shows expected patterns of gene regulation for three native cyprinid species in response to spring and early summer cues.

A comparative ecological genomics framework could permit unparalleled insight into factors that determine environmental and genetic control of spawning in arid-land river fishes and, more importantly, the plasticity of response to altered timing of environmental cues. Most models of global climate change in the American Southwest predict drier conditions, more variable snowpack, earlier spring runoff, and more variability in onset, duration, and magnitude of the monsoon season (Hurd and Coonrod 2007). It appears that species that cue on discharge are most likely to suffer negative consequences of climate change because it is predicted to decouple the autocorrelation of high and low flows, thus diminishing the information content of this cue (Bunn and Arthington 2002; Lytle and Poff 2004).

Table 3. A comparative framework to study abiotic cues, using a microarray approach, focused on three native cyprinid species in the Rio Grande. Abbreviations are (+) genes and/or pathways expected to be upregulated during spring/early summer and discharge spikes, and (-) genes or pathways expected to be downregulated under these same conditions. It is possible to compare these species directly in the field or to manipulate light and turbidity levels under controlled conditions, extract tissues, and conduct microarray experiments. A microarray approach involves isolation of messenger RNA from individuals, conversion to complementary DNA via reverse transcriptase polymerase chain reaction, hybridization of complementary DNA to the array, and quantification of expression patterns of genes on the array via spectral imaging (Wang et al. 2008).

| Species                   | Spawning characteristics       | Photoperiod | Temperature | Discharge spike |
|---------------------------|--------------------------------|-------------|-------------|-----------------|
| Fathead minnow            | Spring/summer; low flow        | +           | +           | -               |
| Rio Grande silvery minnow | Spring/summer; high flow       | +           | +           | +               |
| Red shiner                | Late summer; not flow specific | -           | -           | -               |

### An Uncertain Future

A few years after the publication of *Community and Evolutionary Ecology of North American Stream Fishes* in 1987, fish ecologists were challenged with the task of predicting impacts of previously unrecognized global climate change on freshwater biota. Arid and semiarid catchments are arguably the most vulnerable to alteration of timing and variability of precipitation and discharge (Ragab and Prudhomme 2002) and are of global concern because they comprise roughly one-third of the total land surface area (Jackson et al. 2001). The Rio Grande, for example, is predicted to have lower average winter snowpack and earlier snowmelt runoff along with higher variability in the timing and magnitude of summer monsoon rains (Hurd and Coonrod 2007), which will affect timing and magnitude of abiotic stimuli for fish reproduction. Biological responses to altered timing, magnitude, and duration of surface water flows are likely to be both ecological and genetic in nature (Bunn and Arthington 2002; Lytle and Poff 2004), which suggests the need for integrated research efforts to characterize and predict these responses. However, there is still much to do to successfully translate spatial and temporal distributional patterns into mechanisms and processes that dictate community structure and interactions of YOY fishes. Such understanding will be facilitated by focused and detailed long-term studies of reproductive phenology of river fishes, especially when they are coupled with intensive ecological and, ultimately, comparative genomic study.

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